Fear, Fleeing, and Survival: Human impacts on ground squirrels in an urban-adjacent park

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Fear, Fleeing, and Survival: Human impacts on ground squirrels in an urban-adjacent park

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Dedication

I dedicate this dissertation to those who always believed in me but could not be here to celebrate. I will always love you Josephine & Samuel Wallen, Yolanda & Vicente Ortiz-Chirinos, and Samantha Jimenez.

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Abstract

As the human population continues to grow, anthropogenic pressures impose unprecedented environmental modifications at both large spatial and temporal scales. Wildlife populations must cope with human-induced rapid environmental change (HIREC) not only in highly developed urban areas, but also in more natural landscapes, including parks and reserves. While natural predators elicit a fear response in prey animals, recent studies have shown that human presence can also induce a fear response, which in some cases even exceeds that triggered by natural predators. However, fear of humans may vary among species. Consequently, humans may play an important role in providing small prey mammals spatial and temporal refuge from predators. Here, I explored how humans influence behavior, perceived risk, and apparent survival in the California ground squirrel (*Otospermophilus beecheyi*). In Chapter 1, I conducted repeated tests on multiple individuals in nature to quantify the repeatability of initial escape tendencies, behavior during the escape and latency to resume activity to an approaching human. I also explored whether these stages of the antipredator response are correlated and influenced by individuals previous experience with humans. Chapter 2 explores how squirrels' perceived risk changes in response to drastic changes in human space use caused by a global pandemic. Our goal was to explore the direct and indirect effects humans and natural predators have squirrels' landscape of fear, considering other important environmental factors. Lastly, Chapter 3 examines how survival and permanent emigration are influenced across a human dominated landscape. To gain a comprehensive understanding of the effects of humans on wildlife, I took an integrative approach that considers the diverse factors that determine variation in behavior, perceived risk, and the fitness consequences of these responses.

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Behavioural correlations across multiple stages of the antipredator response: do animals that escape sooner hide longer?

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Abstract

A fundamental assumption in predator–prey ecology is that prey responses comprise two main stages: escape when attack occurs or appears imminent and avoid the threat by seeking refuge until it has passed. While numerous studies have examined either initial prey responses to an approaching predator (flight initiation distance, FID), or subsequent hiding behaviour (e.g. latency to resume activity), to our knowledge, no previous studies have repeatedly tested multiple individuals in nature to quantify whether initial escape tendencies, behaviour during the escape and latency to resume activity are repeatable, and whether these stages of the antipredator response are correlated. The goal of this study was to explore how consistent spatial differences in rates of human activity shape risk-sensitive behaviour throughout multiple steps of the antipredator response (to humans) in California ground squirrels, *Otospermophilus beecheyi*, tested in various group sizes and environmental contexts across time. Our study provides the first example showing that, as predicted: FIDs, latencies to resume activity and other post-FID aspects of prey responses were repeatable and positively correlated at the among-individual level. This correlation is ecologically important in that it provides an underlying mechanism for a trade-off involving not only the cost versus benefit of early versus late escape, or early versus late emergence from refuge, but for a trade-off based on variation in fearfulness expressed across stages. Furthermore, we found that human activity influenced some, but not all, stages of the antipredator response.

Introduction

To understand predator impacts on prey and, in particular, nonconsumptive effects of predators on prey (Peacor et al., 2020; Preisser et al., 2005), a key issue is to elucidate factors that explain variation in prey responses to perceived predation risk (Brown & Kotler, 2004; Creel & Christianson, 2008; Lima, 1998; Wirsing et al., 2021). The overall prey response is commonly split into two main stages: escape when an attack occurs or appears imminent and avoid the threat often by staying in or near refuge (Heithaus et al., 2009; Lima & Dill, 1990). Although this basic framework has long been part of standard predator–prey behavioural ecology, most studies have either quantified escape responses (e.g. flight initiation distances (FIDs); Møller et al., 2016; Stankowich & Blumstein, 2005), or refuge use (e.g. time spent in refuge; Cooper & Sherbrooke, 2015). Surprisingly, few have examined both for the same individuals, particularly in the field. Here, we repeatedly quantified the responses of individually marked, free-ranging animals to the approach of a human. Specifically, we tested for consistent individual differences in multiple stages of the overall prey response to risk (i.e. initial escape tendencies, behaviour during the escape and latency to resume activity after spending time in refuge).

When prey first detect a potential predator, they can, but often do not, immediately initiate an escape attempt. Instead, prey often monitor the predator's behaviour and only initiate escape when the predator approaches more closely. A standard metric for assessing fear is thus an animal's flight initiation distance (FID), the distance at which an individual flees from an approaching intruder. Theory predicts that because active escape from predators has costs (e.g. energy and lost opportunities), prey should typically not initiate escape as soon as they detect predators but should instead optimize their FID by fleeing only when predators have come close enough that the costs of not fleeing are higher than the costs of escaping (Ydenberg & Dill, 1986). The literature (e.g. Dill & Frid, 2020; Møller et al., 2016; Morelli et al., 2019; Stankowich

& Blumstein, 2005) show that FIDs can depend on characteristics of the predator (e.g. greater FID if predators are perceived to be more dangerous), the prey (e.g. the prey's state, escape ability or behavioural type), the social context (e.g. presence of conspecifics) and the ecological context (e.g. availability and distance of refuge). With regard to prey traits, the current interest in animal personalities (Réale et al., 2007; Sih, Bell, & Johnson, 2004; Sih, Bell, Johnson, & Ziemba, 2004) suggests a need to measure consistent individual differences in FIDs; however, to date, relatively few studies have quantified the repeatability of FIDs in nature (but see Cabrera et al., 2017; Carrete et al., 2009; Møller & Tryjanowski, 2014).

Upon fleeing from predators, animals have subsequent decisions to make, including whether to run into shelter and, if so, when to emerge. Rather than running to shelter, animals sometimes flee and then 'stop and look', apparently to reassess the danger. The distance that they flee before they 'stop and look' can be used as an additional measure of fearfulness (i.e. more fearful animals likely have a larger 'stop and look' distance). If prey flee to shelter, then a key decision is when to emerge to resume activity (Cooper & Frederick, 2007; Sih, 1992). More fearful animals likely have a longer latency to resume activity (Bókony et al., 2012; Cooper & Sherbrooke, 2015). While FIDs have been measured in many species (Bonenfont & Kramer, 1996; Engelhardt & Weladji, 2011; Møller & Tryjanowski, 2014; Petelle et al., 2013; Stankowich & Blumstein, 2005; Uchida et al., 2015), fewer studies have explored post-FID responses (but see Bonenefont & Kramer, 1996; Breck et al., 2019; Cooper & Sherbrooke, 2015; Tätte et al., 2018) and, to our knowledge, no studies have quantified consistent individual differences (repeatability) of post-FID responses – either in isolation or in relation to other components of the antipredator response.

If FIDs, ‘stop and look’ distances and latency to resume activity all reflect differences among individuals in underlying fear, then consistent individual differences in these should be positively correlated. These correlations are ecologically important; for example, the core idea that more fearful animals suffer greater opportunity costs (e.g., greater reductions in feeding rate) from avoiding predators hinges not just on them escaping more readily to shelter, but crucially, on them hiding, often for long periods, before resuming activity. However, animals may compensate for the cost of escaping early by having shorter hiding times before resuming activity; in that case, we would expect a negative correlation between FID and post-FID behaviour. It is thus striking that, to our knowledge, no previous studies have tested the hypothesis that larger FIDs are positively or negatively correlated with longer or shorter latencies to resume activity. Ideally, analyses of multistage prey responses to predators should test for effects of both individual differences in behavioural tendencies and multiple aspects of the context (ecological and social) on each stage of the overall response; however, as far as we know, no previous studies have attempted to test this.

We studied the responses of focal animals to approaching humans. With the global expansion of human presence, animal responses to human activity can have important effects on individual and species success (Arroyo et al., 2017; Strasser & Heath, 2013). How well animals cope may depend on a variety of factors, including their behaviour and/or their past experience with human disturbance (Lapiedra et al., 2017; Sih et al., 2011, 2012). In many cases, animals respond to humans as predators, actively avoiding areas of human activity (Clinchy et al., 2016; Oriol-Cotterill et al., 2015; Suraci et al., 2019). In other cases, however, repeated exposure to humans leads to habituation (Blumstein, 2016; Geffroy et al., 2015; Uchida & Blumstein, 2021; Stankowich & Blumstein, 2005). The reduced fear of humans can be associated with a general increase in boldness, exploration or aggressiveness as often seen in animals in urban environments (Breck et al., 2019; Miranda et al., 2013; Møller et al., 2008; Rodriguez-Prieto et al., 2008; Uchida et al., 2015). However, whilst behavioural adjustments in animals inhabiting urban environments are well documented, less is known about how human activities shape behaviour or behavioural variation in animals residing in natural areas, such as reserves or parks that are comparatively insulated from urban disturbance (Corsini et al., 2019; Gonson et al., 2016; Watson et al., 2016).

Here, we examined how variation in rates of human activity shape risk-sensitive behaviour throughout multiple steps of the antipredator response in a free-living mammal, the California ground squirrel, *Otospermophilus beecheyi*. Ground squirrels are ecosystem engineers, a major prey species in the California grasslands (Smith et al., 2016) and display a suite of behavioural responses to threats (Ayon et al., 2017; Hanson & Coss, 1997; Owings & Ledger, 1980; Putman et al., 2015), including human approach (Hammond et al., 2019). While ground squirrels are often deemed pests by humans, they are generally not directly killed by humans. This species therefore offers an interesting opportunity to examine how animals exposed to varying levels of human activity adapt their behaviour in the presence of humans. Specifically, we repeatedly recorded both the squirrels' FIDs (Bjørvik et al., 2014; Uchida et al., 2015; Ydenberg & Dill, 1986) and their post-FID behaviours as discussed above (Fig. 1). Thus, our study is unique in allowing us to both (1) explore how human activity influences each decision of a squirrel's antipredator response (i.e. when to flee and whether and how long to shelter) and (2) examine the covariation between different components of the antipredator response. We predicted that human activity would influence multiple components of a squirrel's risk sensitivity and antipredator response, in that, squirrels who experience high human activity have become habituated to nonthreatening human disturbance and, thus, allow humans to approach closer. If correlated, a decrease in risk sensitivity to human approach will carry over to other components in the antipredator response. We further predicted that if stages of the antipredator response are correlated, then an individual's FID response should also correspond to its risk sensitivity across other contexts, such as their willingness to enter a trap across multiple potential trapping sessions. Finally, we also examined other factors that might contribute to risk-sensitive decision making, including age and sex of the focal individual, the surrounding microhabitat features, and conspecific presence.

Methods

Study Site and Subjects

We studied free-ranging ground squirrels at Briones Regional Park in Contra Costa County, California, U.S.A. (37.93°N, 122.13°W, elevation: 319 m above mean sea level). For this study, we focused on a 0.96 ha site that is a well-known picnic and resting area near a main entrance to the otherwise less human-disturbed 2476 ha Briones Regional Park (Appendix, Fig. A1). Since 2013, we live-trapped, marked and released 868 individuals of known age, sex, reproductive state and mass on a biweekly schedule (see Smith et al., 2018 for details). We recorded the proportion of days an individual was trapped on available trapping days per season (henceforth 'trappability'). Squirrels were individually fur-marked, and on weeks when trapping did not occur, trained observers identified individuals from a distance using binoculars to record spatial locations (see Smith et al., 2018 for details). Owing to the landscape at the site, observers were able to accurately identify individuals from greater than 30 m with binoculars and stood on higher ground to gain a better view of the unique markings when the focal individual was in tall vegetation. Identity was further confirmed by a second observer prior to the start of the trial. For the present study, we focused on the antipredator responses of 88 individuals tested in 2018 and 2019. We combined all spatial data from May to July of these 2 years to determine each squirrel's home site, or the locations where each individual squirrel spent the majority of its time. Locations of trapped and free-living squirrels were noted daily based on a standard set of natural (e.g. burrows, trees) and artificial (e.g. picnic tables, outhouse) landmarks at the study site. We quantified human activity by counting the number of humans present within 15 m of each landmark (Hammond et al., 2019). Following van der Marel et al. (2019), we calculated human activity at each location by dividing the number of humans at a location by its total observation time each summer (henceforth 'home site human activity score'). Within our site, human activity ranged over a spatial gradient going eastward from moderately high to low (Appendix, Fig. 1.1).

Flight Initiation Distance Trials

Between the hours of 0900 and 1400, we selected subjects for FID trials using a regular sampling regime to increase the evenness of sampling across subjects (Altmann, 1974). Focal squirrels were only chosen while foraging and not moving (e.g. walking or socializing) to isolate responses to human approach.

Prior to each assay, the walker noted the location, date, time of day, number of conspecifics present and vegetation cover. We considered conspecifics to be present when they were within 5 m of the focal individual; this is the distance over which this species is most sensitive to environmental changes (Leger et al., 1983; Ortiz et al., 2019). We categorized vegetative cover as high when it effectively covered the body of adults foraging quadrupedally and as low when it did not (low = 0–10 cm; high >10 cm) (Ortiz et al., 2019; Owings & Coss, 1977).

The walker approached the focal subject at a speed of 0.5 m/s (Runyan & Blumstein, 2004). All walkers were trained to ensure consistent speed and posture. Each walker dropped one marker at their departure location and a second marker at the exact moment the squirrel fled (Fig. 1.1). The distance between the focal squirrel and the flight marker was then measured (± 0.1 m). We also noted the distance between the focal squirrel and (1) the walker's starting location (henceforth 'starting distance') and (2) the subject's nearest burrow (henceforth 'distance from shelter') since these influence FIDs in other species (Bonenfant & Kramer, 1996; Engelhardt & Weladji, 2011).

After the initial flee response, observers continued to watch the focal squirrel to record its behaviour. Squirrels typically took one of two options as their post-FID response: (1) fled into shelter and re-emerged after some period of time or (2) fled and stopped to watch at a distance. If a squirrel ran into shelter, we then recorded how long it took to re-emerge from shelter (henceforth 'shelter emergence time'). If a squirrel did not run into shelter, we recorded the total distance it fled from the walker (henceforth 'stop and look distance'). While squirrels could 'stop and look' at a burrow and then proceed into shelter, this rarely occurred. Thus, for our analysis, we only used the squirrel's initial and immediate response to human approach. Individuals were only tested once within a day and, on average (± SE), 5.5 ± 5.2 days passed between trials within a year (range 1–28 days).

Statistical Analysis

Analysis was conducted in R v.3.6.2 (R Core Team, 2020) using the Bayesian package 'brms' (Bürkner, 2017), an interface to Stan (Stan Development Team, 2015) for generalized linear mixed-effects models. We used relatively uninformative priors and four chains and ran models for 10 000 iterations with 1000 warm-up. We used posterior predictive checks and trace plots to check for adequate mixing and model fit. All models converged with low among-chain variability (Rhat = 1). FIDs were square root transformed prior to analysis to meet model assumptions of normality of residuals. We report posterior means for all estimated parameters with 95% credibility intervals (CIs).

Flight initiation distance analysis

We first examined the effects of social and environmental factors on FIDs. Specifically, we ran a univariate mixed model with the following predictors: year, life stage (juvenile or adult), sex, individual trappability, trial number, number of conspecifics present, vegetation cover, starting distance, home site human activity score and distance to shelter. We included home site identity, walker identity and squirrel identity nested within home site identity as random intercepts. Home site identity was included as a random intercept because multiple squirrels were tested from the same home site and thus would more likely be similar to each other. Walker identity was included to control for potential experimental variation arising from differences among walkers. Finally, we recognized that in scenarios where individuals were tested in the presence of other conspecifics simultaneously, the FID of these individuals were not independent. Thus, we reran our model after filtering the data to only include the FID of the first individual to flee within these group testing situations but found that the same predictor effects remained as in our full data set model (Appendix, Table 1.1).

Individual FID repeatability (R_{FID}) was calculated by extracting the variance components from our full FID model and using the following standard formula (Nakagawa & Schielzeth, 2010; Stoffel et al., 2017):

$$R_{\mathrm{FID}} = \frac{V_{\mathrm{ind}}}{(V_{\mathrm{ind}} + V_{\mathrm{home}} + V_{\mathrm{obs}} + V_{\mathrm{res}})}$$

where V_{ind} is the among-individual variance, V_{home} is the among-home site variance, V_{obs} is the among-observer variance and V_{res} is the residual variance.

Post-flight initiation distance response and correlation analysis

Given that squirrels took only one of two escape options, we first ran a beta-binomial model exploring the factors that influenced whether a squirrel sheltered or not (Appendix, Table 1.2) and then we ran separate bivariate models to analyze these disparate post-FID responses and their among-individual correlations with FID. Specifically, one model contained FID and shelter emergence time as response variables, and the second model contained FID and stop and look distance as response variables. Shelter emergence time and stop and look distance were both modelled using a gamma distribution and log link function. Both bivariate models contained the same set of predictors (year, sex, life stage, trial number, home site activity score and trappability). Walker identity and squirrel identity were included as random intercepts. To estimate the correlation between an individual's FID and post-FID response, we extracted the posterior mean among-individual random intercept correlation from each model, respectively. We also estimated the repeatability (R) of each post-FID response by extracting the variance components from their respective models and using the following formula for gamma-distributed variables (Nakagawa et al., 2017):

$$R = \frac{V_{\text{ind}}}{V_{\text{ind}} + V_{\text{obs}} + \ln\,(1 + \frac{1}{\upsilon})}$$

where V_{ind} is the among-individual variance, V_{obs} is the among-observer variance and υ is the shape parameter of the gamma distribution.

Ethical Note

All methods used were approved by the Animal Care and Use Committees of Mills College and the University of California Davis (No. 19853). Procedures used for this study are consistent with guidelines of the American Society of Mammologists for the use of wild mammals in research (Sikes, 2016). Research permits were obtained from the California Department of Fish and Wildlife, Sacramento, California, U.S.A. and the East Bay Regional Park District, Castro Valley, California, U.S.A. On trapping days, Tomahawk live traps were covered with cardboard to provide shade and checked at 30 min intervals. Once trapped, squirrels were then placed in a cone-shaped, cloth handling bag to reduce stress of the animals (Koprowski, 2002; Hammond et al., 2019). Squirrels remained in the handling bag for processing (i.e. obtain mass and sex) and marking and then released at the exact location they were trapped.

Results

Flight Initiation Distance

We conducted 384 FID trials on 88 unique ground squirrels over the 2 years (2018, 2019: juvenile females: $N = 21, 16$; juvenile males: $N = 11, 7$; adult females: $N = 20, 23$; adult males: $N = 6, 6$; 22 individuals were tested in both 2018 and 2019). A total of 10 walkers were trained and used in the analysis. The mean (± SE) FID for both years combined was 8.6 ± 4.8 m (range 0.04–23.81 m). For individuals sampled more than once within a summer ($N = 85$), there was a mean replication of six trials per individual in 2018 and four trials per individual in 2019. For FID trials conducted on groups ($N = 35$), we sampled an average of 2 ± 0.06 individuals from each group.

We found FIDs were repeatable (*R* = 0.29; 95% CI [0.172, 0.409]). Human activity within an individual's home site predicted its FID; squirrels experiencing greater human activity had shorter FIDs; i.e. were bolder (Table 1.1, Fig. 1.2a). Highly trappable individuals also had shorter FIDs than less trappable individuals (Table 1.1, Fig. 1.2b). FIDs increased with group size (Table 1.1, Fig. 1.2c), suggesting squirrels were quicker to flee from an approaching human when more conspecifics were present. Females had shorter FIDs than males (Table 1.1, Fig. 1.2d). We also found that squirrels had longer FIDs with longer starting distances (Table 1.1). Lastly, we found year had a significant impact on FID, with squirrels having shorter FIDs in 2019 than in 2018 (Table 1.1).

Post-flight Initiation Distance Response and Correlation

Squirrels ran into shelter in 30% of trials. Juveniles sheltered (as opposed to 'stop and look') more frequently than adults (Appendix, Table 1.2). Squirrels tested near a burrow were more likely to run into shelter (Appendix, Table 1.2), but no other factor significantly explained variation in likelihood of running to shelter. Notably, the decision to run into shelter was not repeatable (*R* = 0.038 [0, 0.119]), but time to emerge from shelter was repeatable (*R* = 0.435 [0.168, 0.676]). Individuals from home sites that experience greater human activity emerged from shelter more quickly than squirrels from home sites with lower human activity levels (-2.336 [-4.413, -0.431]; Fig. 1.3a, Appendix, Table 1.3). Furthermore, more trappable individuals had shorter shelter emergence times than less trappable individuals (-1.359 [-2.456, -0.359]; Fig. 1.3b, Appendix, Table 1.3). We also found a positive among-individual correlation between emergence time from shelter and FID (0.57 [0.139, 0.967]; Fig. 1.4a), indicating that individuals that allowed walkers to approach more closely before fleeing were also faster to re-emerge from shelter. Time to emerge from shelter decreased with trial number (0.137 [0.030, 0.241]; Appendix, Table 1.3).

The response to stop and look from a distance occurred in 70% of trials (mean ± SE stop and look distance: 5.1 ± 0.3 m; range 0.2–27.7 m). Stop and look distances were only weakly repeatable (*R* = 0.216 [0.073, 0.370]), and we found no significant predictors for stop and look distance (Appendix, Table 1.4). However, we did find a positive among-individual correlation between stop and look distance and FID, suggesting that individuals that allowed walkers to approach more closely before fleeing also fled shorter distances from the walker following their FID response (0.736 [0.428, 0.988]; Fig. 1.4b).

Discussion

Our study shows that variation in human activity can profoundly affect multiple aspects of risk sensitivity and antipredator responses in wildlife even over relatively small spatial scales. Specifically, ground squirrels residing in areas of greater human activity consistently had shorter FIDs than squirrels residing in adjacent, nearby areas of lower human activity. Importantly, repeated exposure to human activity also influenced the post-FID shelter response, as squirrels from high human disturbance areas were consistently faster to emerge from shelter. Furthermore, since FID and the post-FID responses were correlated, squirrels fled shorter distances before stopping to observe a potential threat following their flight response. Squirrels from high activity sites have likely habituated to high human activity, thus responding less to an approaching human compared to individuals that have less experience with humans. While many other studies have observed animal habituation to humans (Petelle et al., 2013; Uchida & Blumstein, 2021; Uchida et al., 2019; Vincze et al., 2016), it is striking that variation in the degree of habituation emerged over a small spatial scale (i.e. within a 1 ha area). Beyond the strong effects of relative human activity on multiple antipredator behaviours, we also documented consistent individual differences in the suite of repeatable behaviours along a general, shy–bold continuum (Wilson et al., 1994), including high among-individual correlations between FID and post-FID responses for the first time.

Having a highly correlated suite of behaviours may be adaptive or maladaptive, depending on the situation and environment in which the animal resides (Geffroy et al., 2015; Trouilloud et al., 2004; Wilson et al., 2020). In this case, having correlated behaviours throughout the antipredator response may be beneficial when encountering predators (e.g. when real danger is present, animals should both flee readily and hide for a relatively long time before resuming activity). However, the correlation may exacerbate unnecessary over-avoidance of humans that can be a substantial problem in human-disturbed environments (Guiden et al., 2019; Trimmer et al., 2017). Unhabituated animals might both flee too readily from nonthreatening humans but also wait too long to emerge from shelter, which may mean a lost foraging opportunity. On the other hand, getting habituated in terms of both reduced tendency to flee and reduced time spent inactive can be beneficial. However, if boldness (here, when habituating to humans) carries over to other situations, this can be ecologically relevant. For example, we know that bolder squirrels are prone to carrying fleas (Smith et al., 2021) and have increased venom resistance (Holding et al., 2020). Perhaps most notably, it has been suggested that boldness associated with habituation to humans can make animals less wary when encountering actual dangerous predators, which can obviously be very costly (Geffroy et al., 2015; Lowry et al., 2012). Thus, anthropogenic influences on boldness could influence disease transmission and predator–prey dynamics.

Here, we found that animals that were bolder, apparently due to being habituated to human activity, were also more readily trapped. Other studies have found mixed evidence for an association between boldness and trappability (Biro, 2012; Brehm & Mortelliti, 2018; Michelangeli et al., 2015). The observation that trappability predicts antipredator behaviour can have important implications as a systematic bias when trapping for monitoring, ecological research or pest control (Biro & Dingemanse, 2009; Garvey et al., 2020).

Besides strong effects of human activity and individual differences, the three main antipredator responses were largely either unaffected or only weakly affected by the social (presence and number of conspecifics) and environmental (distance to shelter, vegetation cover) contexts that we considered. We predicted that animals closer to shelter would exhibit shorter FIDs and that vegetation cover would affect FIDs, but these factors did not significantly affect FIDs. FIDs were, however, affected by the social context (group size). In theory, this effect could have gone either way. If larger groups with 'many eyes' (Pulliam 1973) detect predators sooner, animals in larger groups should flee sooner (i.e. have larger FIDs). On the other hand, the dilution or confusion effects (Bertram, 1978) can make animals in larger groups safer, in which case, FIDs should be smaller. In fact, FIDs increased with group size, consistent with the former mechanism. This finding is particularly interesting given that adult California ground squirrels are less vigilant when foraging in groups, and all animals – regardless of age or sex – decrease their intensity of vigilance as group size increases (Ortiz et al., 2019). Taken together, this suggests that, on average, individuals foraging in groups may benefit from both increased energy intake and earlier detection of threats. However, humans are not a direct threat to this species, and consistently fleeing early due to human disturbance can lead to decreased energy intake in the long run. Thus, the social information provided from group foraging may only be beneficial when confronted with an actual predator.

We also found evidence for more subtle context dependence in these antipredator behaviours. In particular, after fleeing (post-FID response), the decision to 'stop and look' versus flee to shelter was largely environmentally context dependent. Animals showed no consistent individual differences in this decision. Instead, they were more likely to flee to shelter if it was available nearby. Interestingly, juveniles were generally more likely to flee to shelter rather than 'stop and look'; this presumably reflects their greater vulnerability to predators and, thus, greater fear (Putman et al., 2015).

We found that, on average, females had significantly shorter FIDs than males. We found this to be surprising as a large amount of literature have found either no sex differences in FID (Lemos-Espinal & Smith, 2021; Stankowich & Blumstein, 2005) or have found the opposite, with males having shorter FIDs than females (Garcia-Arroyo & MacGregor-Fors, 2020; Guay et al., 2013). Often, sex differences that do occur are detected during the breeding season; however, our study was performed during the nonbreeding season and at a time where juveniles are weaned from their mothers. Previous studies have found that female California ground squirrels tend to have higher stress levels (Hammond et al., 2019) and larger home ranges (Boellstorff & Owings, 1995) than males. This may suggest that female ground squirrels encounter humans more frequently than males, due to their expansive home range, and thus have become more habituated to humans. More work is required to test this hypothesis. Lastly, we found FIDs in 2019 to be significantly shorter than FIDs in 2018. However, because the 2 years may have differed in many ways (e.g. environmental conditions, squirrel density, rates interactions with humans and predators), we cannot distinguish among these potential explanations for this result.

We believe our findings of high individual level correlation among multiple stages of the antipredator response are consistent with our general conceptual framework, contributing new insights and opportunities for the study of animal personalities. Future research should continue to investigate these correlations throughout the overall antipredator response in other species and the trade-offs animals face across all stages of prey’s response to risk and not just their initial flight response. More broadly, such inquiries may reveal insights into how human-impacted behavioural syndromes affect population dynamics, community interactions and ecosystem functions, and provide more insights into the fundamental processes linking animal behaviour, humans, and ecology.

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Table 1.1. Predator effects on squirrel flight initiation distance (FID)

term	estimate ± SE	95 % CI
(Intercept)	3.053 ± 0.230	(2.611, 3.506)
Year	**-0.347 ± 0.095**	**(-0.534, -0.163)**
Sex (1)	**-0.242 ± 0.113**	**(-0.466, -0.020)**
Life history stage (1)	0.042 ± 0.095	(-0.142, 0.228)
Trial Number	0.011 ± 0.016	(-0.020, 0.042)
Number of conspecifics present	**0.148 ± 0.048**	**(0.053, 0.243)**
Vegetation cover (1)	0.013 ± 0.081	(-0.148, 0.171)
Distance to nearest shelter (m)	0.012 ± 0.011	(-0.100, 0.034)
Starting distance (m)	**0.028 ± 0.006**	**(0.017, 0.039)**
Home site human activity	**-1.184 ± 0.356**	**(-1.909, -0.497)**
Trappability	**-0.452 ± 0.187**	**(-0.820, -0.086)**

Life history stage: juvenile 1⁄4 0, adult 1⁄4 1; sex: male 1⁄4 0, female 1⁄4 1; vegetation: low (0e10 cm) 1⁄4 0, high (>10 cm) 1⁄4 1; random intercepts: focal animal, home site and walker identity. Values include posterior mean estimates ± standard error (SE) with the 95% credible intervals (CIs). Significant predictors are shown in bold.

Figure captions

Figure 1.1 Graphic depicting multiple componenets of the antipredator response.

Figure 1.2 Model predicted relationship between flight initiation distance (FID) and (a) average level of human activity at home site, (b) trappability, (c) foraging group size and (d) sex. Shaded regions in (a) and (b) represent 95% credible intervals. For (c) and (d), the middle quartile (dark line) represents the median; the box edges are the upper and lower quartiles; the whiskers are 50% from the median and the closed circles correspond to the outliers, calculated as the values smaller or larger than 1.5 times the box length (i.e. upper-lower quantile).

Figure 1.3. Model predicted relationship between emergence time and (a) human activity and (b) trappability. Shaded regions represent 95% credible intervals.

Figure 1.4. Among-individual correlations between flight initiation distance (FID) and (a) emergence time and (b) stop and look distance. BLUPs (best linear unbiased predictors, shown as black points) represent posterior means of individual random intercepts extracted from the multivariate models.

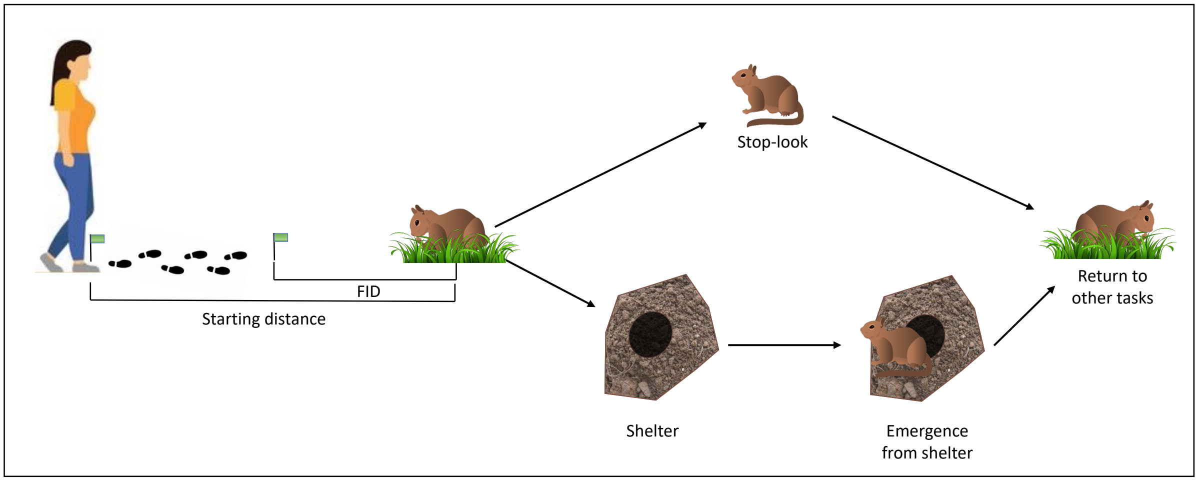
Stop-look
FID
Starting distance
Return to other tasks
Shelter
Emergence from shelter

Figure 1.1.

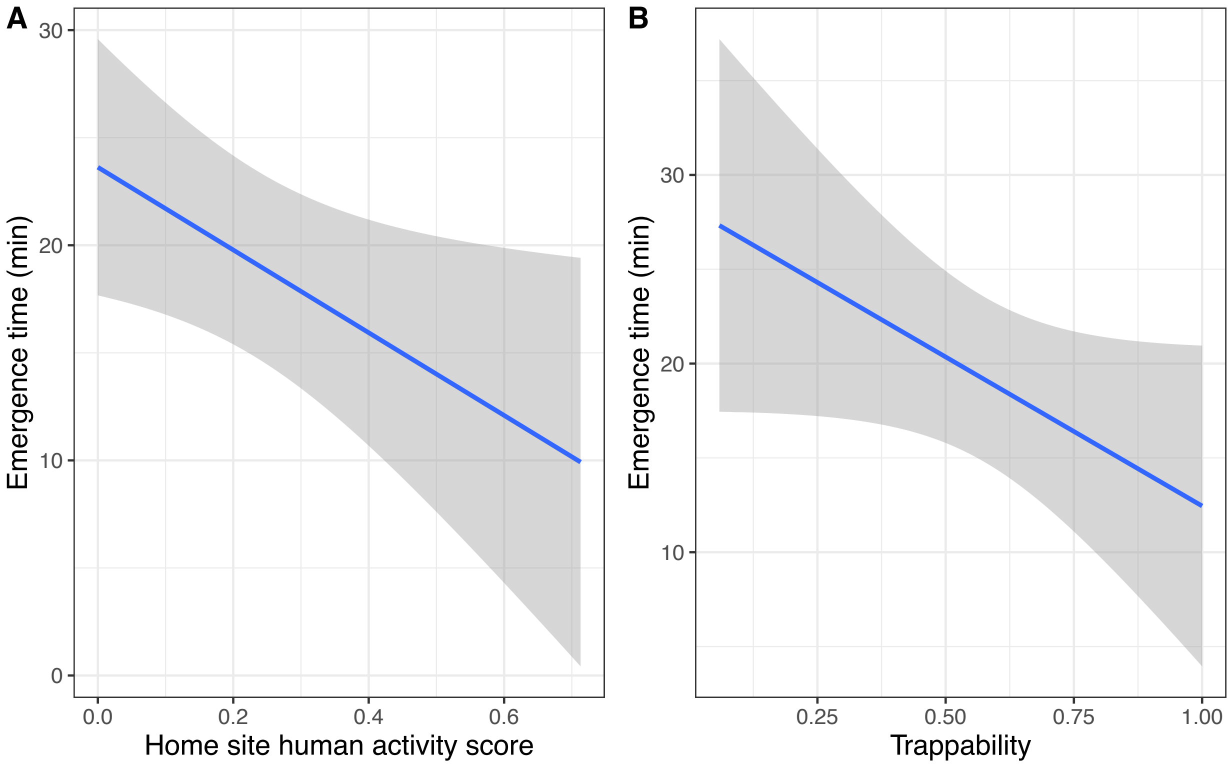
A
B
Emergence time (min)
0
10
20
30
0.0
0.2
0.4
0.6
Home site human activity score
10
20
30
0.25
0.50
0.75
1.00
Trappability

Figure 1.2.

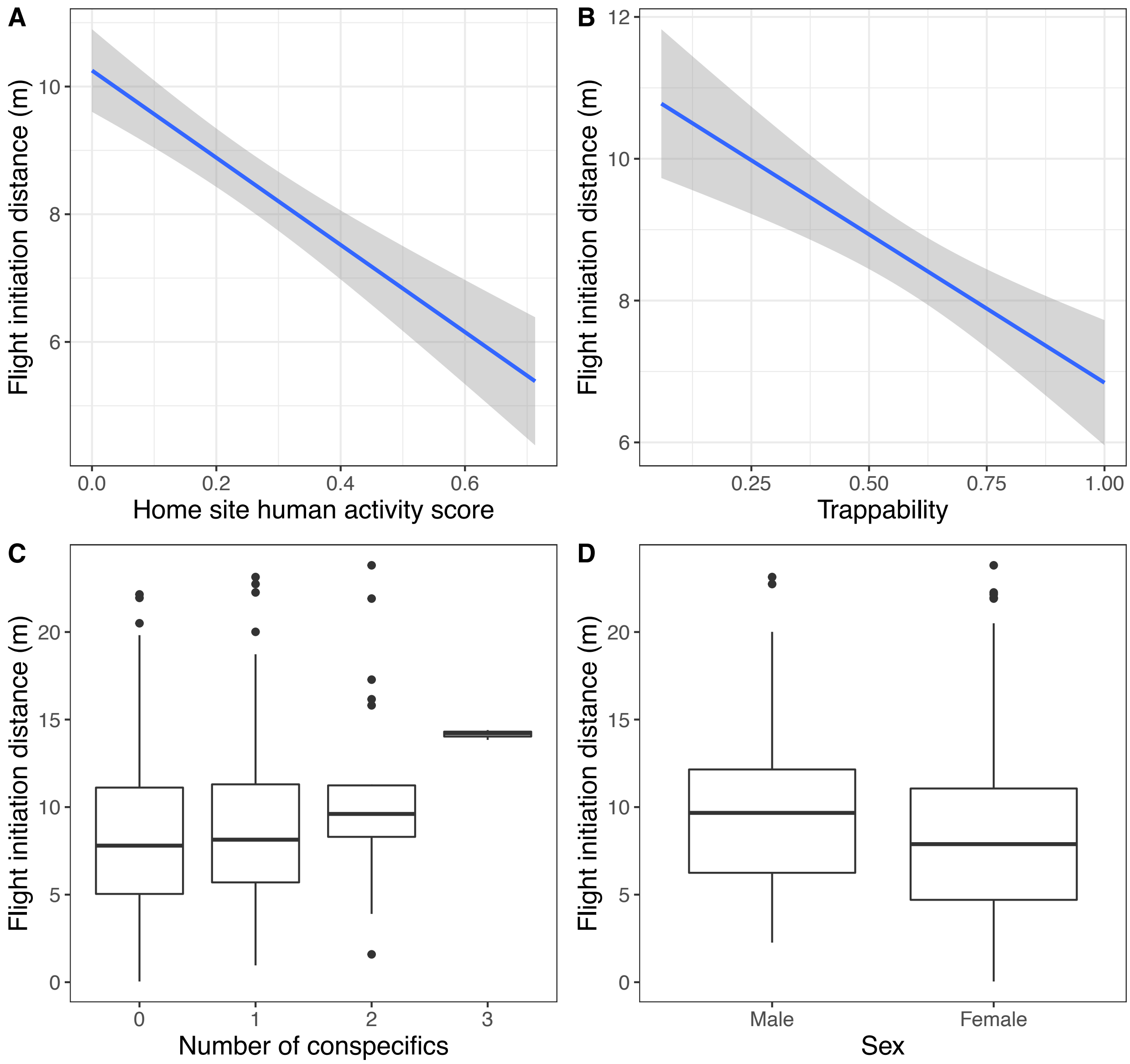
A
Flight initiation distance (m)
10
8
6
0.0
0.2
0.4
0.6
Home site human activity score
B
Flight initiation distance (m)
12
10
8
6
0.25
0.50
0.75
1.00
Trappability
C
Flight initiation distance (m)
20
15
10
5
0
0
1
2
3
Number of conspecifics
D
Flight initiation distance (m)
20
15
10
5
0
Male
Female
Sex

Figure 1.3.

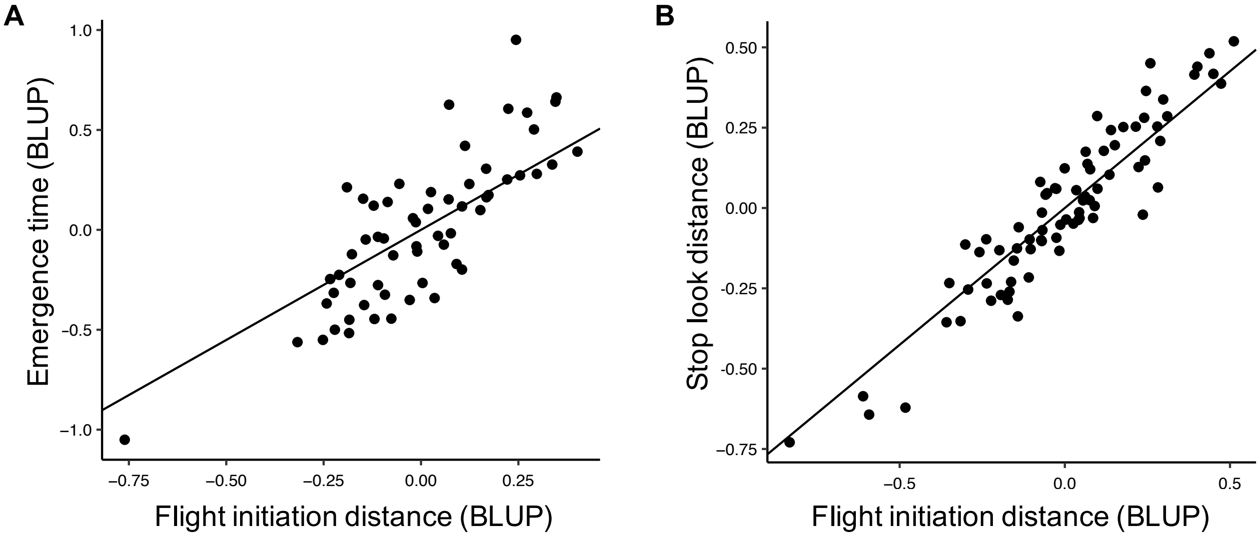
A
1.0
0.5
0.0
−0.5
−1.0
Emergence time (BLUP)
−0.75
−0.50
−0.25
0.00
0.25
Flight initiation distance (BLUP)
B
0.50
0.25
0.00
−0.25
−0.50
−0.75
Stop look distance (BLUP)
−0.5
0.0
0.5
Flight initiation distance (BLUP)

Figure 1.4.

Appendix

Table S1.1. Predictor effects on squirrel flight initiation distance (FID) only including the first individual to flee in a group testing situation. Values include posterior mean ± standard error (SE) with the 95% credible intervals (CIs). Significant outcomes are shown in bold.

term	estimate ± SE	95% CI
(Intercept)	2.995 ± 0.237	(2.527, 3.462)
Year	**-0.295 ± 0.102**	**(-0.495, -0.097)**
Sex (1)	-0.223 ± 0.119	(-0.456, 0.012)
Life history stage (1)	0.045 ± 0.101	(-0.152, 0.245)
Trial Number	0.010 ± 0.017	(-0.024, 0.044)
Number of conspecifics present	**0.172 ± 0.061**	**(0.053, 0.292)**
Vegetation cover (1)	0.005 ± 0.086	(-0.163, 0.173)
Distance to nearest shelter (m)	0.015 ± 0.012	(-0.009, 0.038)
Starting distance (m)	**0.029 ± 0.006**	**(0.018, 0.041)**
Home site human activity	**-1.228 ± 0.376**	**(-1.994, -0.515)**
Trappability	**-0.472 ± 0.197**	**(-0.859, -0.085)**

Life stage: juvenile = 0, adult = 1; Sex: male = 0, female = 1; Vegetation: low (0-10cm) = 0, high (>10cm) = 1; random intercepts: focal animal, home site and walker identity

Table S1.2 Predictor effects on squirrel's decision to shelter for post-flight initiation distance response. Values include posterior mean ± standard error (SE) with the 95% credible intervals (CIs). Significant outcomes are shown in bold.

term	estimate ± SE	95% confidence interval
(Intercept)	-1.150 ± 0.890	(-3.28, 0.210)
Year	-0.410 ± 0.390	(-1.200, 0.340)
Sex (1)	0.460 ± 0.360	(-0.230, 1.190)
Life history stage (1)	**-0.890 ± 0.320**	**(-1.550, -0.280)**
Number of conspecifics present	0.304 ± 0.211	(-0.100, 0.712)
Vegetation cover (1)	-0.190 ± 0.380	(-0.950, 0.540)
Distance to nearest shelter (m)	**-0.110 ± 0.054**	**(-0.220, -0.010)**
Starting distance (m)	0.029 ± 0.025	(-0.020, 0.079)
FID (m)	0.000 ± 0.038	(-0.076, 0.070)
Home site human activity	-0.680 ± 0.970	(-2.710, 1.170)
Trappability	0.780 ± 0.620	(-0.410, 2.060)

Life stage: juvenile = 0, adult = 1; Sex: male = 0, female = 1; Vegetation: low (0-10cm) = 0, high (>10cm) = 1; random intercepts: focal animal, home site and walker identity

Table S1.3. Predictor effects on shelter emergence time modeled with flight initiation distance (FID) in multivariate model. Values include posterior mean estimates ± standard error (SE) with the 95% credible intervals (CIs). Significant predictors are shown in bold.

	term	estimate ± SE	95% CI
Shelter emergence time			
	(Intercept)	3.174 ± 0.511	(2.170, 4.181)
	Year	-0.130 ± -0.289	(-0.704, 0.431)
	Sex (1)	0.248 ± 0.319	(-0.380, 0.868)
	Life history stage (1)	-0.026 ± 0.266	(-0.548, 0.494)
	Home site human activity	**-2.336 ± 1.022**	**(-4.413, -0.431)**
	Trial Number	**0.137 ± 0.054**	**(0.030, 0.241)**
	Trappability	**-1.359 ± 0.532**	**(-2.456, -0.359)**
FID			
	(Intercept)	3.149 ± 0.331	(2.485, 3.793)
	Year	0.043 ± 0.160	(-0.266, 0.362)
	Sex (1)	-0.181 ± 0.159	(-0.485, 0.140)
	Trial Number	0.049 ± 0.028	(-0.004, 0.104)
	Life history stage (1)	0.150 ± 0.133	(-0.112, 0.410)
	Home site human activity	-0.627 ± 0.499	(-1.619, 0.362)
	Starting distance (m)	0.010 ± 0.010	(-0.010, 0.028)
	Trappability	**-0.661 ± 0.262**	**(-1.182, -0.158)**
	Number of conspecifics present	0.069 ± 0.075	(-0.080, 0.212)

Life stage: juvenile = 0, adult = 1; Sex: male = 0, female = 1; random intercepts: focal animal, home site and walker identity

Table S1.4. Predictor effects on stop look distance modeled with flight initiation distance (FID) in multivariate model. Values include posterior mean estimates ± standard error (SE) with the 95% credible intervals (CIs). Significant predictors are shown in bold.

	term	estimate ± SE	95% CI
Stop look distance			
	(Intercept)	2.058 ± 0.284	(1.498, 2.612)
	Year	0.080 ± 0.148	(-0.211, 0.372)
	Sex (1)	-0.179 ± 0.175	(-0.522, 0.167)
	Life history stage (1)	-0.194 ± 0.148	(-0.493, 0.0860)
	Home site human activity	-0.278 ± 0.497	(-1.267, 0.709)
	Trial Number	-0.047 ± 0.028	(-0.103, 0.006)
	Trappability	-0.147 ± 0.298	(-0.745, 0.431)
	Number of conspecifics present	0.118 ± 0.098	(-0.730, 0.314)
FID			
	(Intercept)	3.121 ± 0.270	(2.600, 3.660)
	Year	**-0.517 ± 0.111**	**(-0.736, -0.302)**
	Sex (1)	-0.05 ± 0.128	(-0.306, 0.196)
	Trial Number	-0.009 ± 0.106	(-0.219, 0.193)
	Life history stage (1)	-0.031 ± 0.017	(-0.066, 0.003)
	Home site human activity	**-1.157 ± 0.373**	**(-1.917, -0.453)**
	Starting distance (m)	**0.035 ± 0.006**	**(0.023, 0.047)**
	Trappability	**-0.545 ± 0.214**	**(-0.955, -0.119)**
	Number of conspecifics present	**0.146 ± 0.055**	**(0.039, 0.254)**

Life stage: juvenile = 0, adult = 1; Sex: male = 0, female = 1; random intercepts: focal animal, home site and walker identity

Figure S1.1. Aerial view of study site in Briones Regional Park, Contra Costa County, CA. Human activity varies throughout the site with high average human activity occurring to the left and gradually decreasing moving towards the right.

Human presence alters the landscape of fear for a free-living mammal

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Abstract

Recent studies predict that humans may play an important role in providing small prey mammals spatial and temporal refuge from predators. Global COVID-19 lockdown restrictions offered a unique opportunity to explore how a sudden change in human presence in urban and semi-urban areas impacts wildlife. Here we report on these effects by mapping the spatial distributions of humans and natural predators to characterize the landscape of fear in a COVID and non-COVID year for the California ground squirrel (*Otospermophilus beecheyi*). We used a structural equation modeling approach to explore how human presence, predator presence, and habitat features shape fear responses [e.g., giving-up densities (GUDs), number of foragers, average time foraging, and food intake rate while at food patches]. Partitioning of the direct and indirect effects revealed the important role that humans play in the squirrels' landscape of fear. We found that a COVID-related change in the concentration of human presence within a semi-urban park decreased spatial refuge from natural predators, thereby increasing perceived risk for squirrels during the COVID-19 lockdown. Thus, risk-sensitive foraging depends on a complex interplay between human, dog, and natural predator activity as well as microhabitat features. Our findings elucidate the myriad ways humans directly and indirectly influence animal perception of safety and danger in a changing world.

Introduction

Animals live in environments with spatial and temporal variation in predation risk where a key goal is to locate areas of lower risk (Sih 1987, Lima and Dill 1990, Smith et al. 2019, Wirsing et al. 2021). One major advance in understanding how risk perception varies across space involves mapping prey animal responses across a landscape, broadly referred to as the "landscape of fear" (Iribarren and Kotler 2012, Laundré et al. 2014, Gaynor et al. 2019). This powerful approach links predation risk and other features of the physical landscape to explain spatial variation in prey numbers and risk-sensitive behaviors (e.g., foraging decisions).

Given the expansion of human presence, there is growing interest in understanding landscapes of fear in urban habitats. In many urban parks, the recent COVID-19 pandemic provided a natural experiment for elucidating how human activity affects risk-sensitive behaviors. Human activity was substantially reduced in some parts of parks, while humans continued to visit those that remained open. These changes in human activity may have cascading effects on wildlife behavior, particularly for small prey animals. Recent studies have also shown that human presence can induce a fear response in animals, which in some cases, even exceeds that of natural predators (Ciuti et al. 2012). In contrast, many prey animals may not fear humans but instead exploit spatial and temporal refuge caused by predators avoiding humans; for example, some prey actively forage at times of the day when human activity reduces predator activity (Suraci et al. 2019).

Small mammals experience considerable temporal and spatial variability in predation risk, and these risks are reflected by foraging decisions (Kotler et al. 1991, Jacob and Brown 2000, Orrock et al. 2004). A useful tool for assessing spatial variation in perceived risk involves measuring relative exploitation of an array of depletable food patches. This experimental approach yields information on spatial variation in giving-up densities (GUDs; i.e., the amount of food remaining in a patch). A higher GUD at a given location indicates increased risk. By mapping surrounding environmental factors (e.g., spatial variation in predator activity or habitat features), we can assess how these factors affect perceptions of risk. Giving-up densities thus offer a useful tool for investigating adaptive foraging decisions, reflected by measures of habitat preference, perceived predation risk and interspecific competition (Bedoya-Perez et al. 2013).

Although many studies have used giving-up densities to assess population-level foraging decisions across a landscape of fear (Kotler 1997, Toscano et al. 2016, Juliana et al. 2017, Menezes et al. 2019), few have information on the behavioral decisions of individual animals at each foraging patch during these experiments. The key point being that while studies have often measured GUDs across a landscape (Brown 1988, Kotler 1997, Bedoya-Perez et al. 2013), these GUDs often represent the end result of multiple visitors foraging at each patch for varying amounts of time. Relative safety at patches is then reflected by variation in: 1) local forager (prey) density; 2) number of unique foragers visiting a patch both due to variation in local density and in visit rate above and beyond local density; 3) average time foraging per visit; and 4) food intake rate while at the foraging patch.

The first aspect can be assessed through local population density near a given patch. Individuals have the option to go to an area within the landscape or avoid it due to perceived levels of risk. Spaces where individuals perceive lower risk are likely to be visited more frequently and thus have higher local densities. Second, even if an individual deems an area ‘safe to visit’, that does not necessarily mean that it will consider a particular patch ‘safe to forage’. For example, even if a general area has enough refuge to attract a high local density of animals, foraging patches that are farther from refuge may receive fewer visits. Thus, measuring the number of unique individuals to visit and actively forage at a food patch provides us with additional information regarding fear expressed within a population. The null hypothesis is that, all else being equal, increased local density should be associated with a higher number of individuals visiting a food patch. Yet, characterizing the factors that influence an individual to visit a food patch above and beyond local squirrel density can provide finer scale insights into the landscape of fear.

Measuring the average time that individuals spend foraging at a patch per visit provides another assessment of perceived risk. Food patches where individuals take more time to actively forage may reflect lower perceived risk than those which individuals visit only briefly. A food patch visited by multiple individuals (e.g., because local density is high) but for a short duration per visit provides a different level of information than a food patch visited by fewer individuals for longer periods of time. Finally, animals can vary their food intake rate while visiting a patch. If predation risk causes them to be more vigilant this can reduce their food intake rate while at a patch. Conversely, risk might induce some prey to feed faster to reduce their duration of risky exposure at the foraging patch.

Here we conducted a multi-year experiment exploring the landscape of fear for the California ground squirrel (*Otospermophilus beecheyi*) in a semi-urban park with varying rates of human presence, natural predator presence, and microhabitat features. Our studies were performed in both 2019, the year before the global COVID-19 pandemic and 2020, the first year of the pandemic. Our overall goal was to quantify the multiple aspects at which prey can express fear. Here we refer to the ecologists' concept of fear measured by behavioral avoidance of perceived risks as opposed to an emotional or physiological response (Zanette and Clinchy 2019, Ortiz-Jimenez et al. 2022). Nonetheless, it is important to note that work in our study populations explicitly link risk-sensitive behaviors to physiological fear responses (Hammond et al. 2019). In the current field experiment, we focused on how the spatial distributions of human & dog activity as well as those of squirrels' diurnal predators (raptors and rattlesnakes) and key habitat features (burrows, ground cover, sky cover) contribute to variation in (1) GUDs, (2) number of foragers, (3) amount of time spent foraging, and 4) foraging rate. We used a structural equation modeling approach to quantify direct and indirect relationships among these variables and explore their contrasting relationships in 2019 and 2020.

In the non-COVID year, we predicted that humans would provide areas of refuge for prey from predators (i.e., squirrels feel safer to visit and forage in areas of higher human activity). Moreover, we expected to see a negative spatial correlation between humans and the squirrel's active predators. Further, we expected habitat to play an important role in perceived risk by squirrels. Most obviously, we predicted that distance to refuge (burrow entrances) would have a strong effect on risk with squirrels avoiding areas farther from refuge. We further predicted that areas with low vegetation would be associated with higher perceived risk from ground predators (Ortiz et al. 2019), and that areas of low sky cover would be associated with higher risk perception from raptors. In contrast, in the COVID year, we expected a decrease in human activity to be associated with changes in activity of the squirrel's active natural predators and local squirrel density. Specifically, in the COVID year, we expected a weaker effect of humans on spatial variation in GUDs and a concomitantly stronger effect of natural predators and habitat features that affect risk from natural predators.

Methods

Study site and subjects

Since 2013, we have annually studied free ranging California ground squirrels at Briones Regional Park in Contra Costa County, California, U.S.A. (Latitude: 37.93 North, Longitude: 122.13 West, Elevation: 319 m above mean sea level). Our study site resides in an old walnut grove nearby a popular hiking trail. Within the site, a restroom area and waterspout are located at the southern end near the trail entrance leading to moderate foot traffic within the site from humans; however, the southern end of the site has fewer human amenities and thus less visitation. The surrounding habitat at the study site consists primarily of open oak savannah interspersed with more heavily vegetated riparian corridors (Ortiz et al. 2019).

This facultatively social species spends most of its day above ground and seeks safety in underground burrows to escape from a wide range of predators including rattlesnakes (*Crotalus oreganus*), coyotes (*Canis latrans*), red-tailed hawks (*Buteo jamaicensis),* Cooper's Hawks (*Accipiter cooperii*), and white-tailed kites (*Elanus leucurus*)(Smith et al. 2016). Ground squirrels forage on a range of food items which vary spatially and temporally throughout the season; however, seeds and plant parts make up the majority of their diet (Smith et al. 2016).

Within our study site we monitored California ground squirrels from the end of May to early August during annual periods of increased activity of both juveniles and adults above ground (Smith et al. 2018). Individual ground squirrels were trapped using Tomahawk live-traps on a biweekly schedule and individually marked using a Monel ear tag and injected with a Passive Integrated Transponder (PIT) tag (Biomark Inc., Idaho, Nebraska, USA) for accurate long-term identification (see Smith et al. 2018 for details). After processing, ground squirrels were released immediately after processing at their capture location. All procedures were approved by the IACUC Committee at Mills College and the University of California at Davis

IACUC protocol #19853 and are consistent with the guidelines of the American Society of Mammologists for the use of wild mammals in research (Sikes 2016).

Spatial observations

Observations were conducted on most summer weekdays when trapping and GUD experiments did not occur and during the morning and early afternoon (0800-1300 h), when California ground squirrels, most of their main natural predators, and humans are most active. During our observations, we recorded space-use patterns of marked squirrels, noting visits within less than 5 m of natural and human-made landmarks (e.g., trees, picnic benches, bathroom, etc.)(Gall et al. 2022). For humans and predators, we focused only on the activity levels for those species that were consistently active during our sampling period, such as rattlesnakes, raptors, humans, and dogs. Coyotes are mainly nocturnal at our study site, with peaks in activity outside of our experimental time (unpublished camera trap data). During our daytime observation periods, we only saw coyotes on 10 days in 2019 and 3 days in 2020.

Our field site is subject to moderate levels of disturbances, including foot traffic by both humans and dogs (Hammond et al. 2019). On- and off-leash dogs are seen regularly at our site, especially during the summer months (Smith et al. 2018). To quantify the distribution and activity of different visitors (i.e., rattlesnakes, raptors, humans & dogs), we calculated visitation rates at landmarks spread around the study site. For each landmark, we counted the number of individuals of each disturbance type present within 15 m of a landmark on a specific day (Gall et al. 2022) and divided this number by the total observation hours per day. We then took an average from all observation days throughout the season to yield annual activity scores for each species at each location (Ortiz-Jimenez et al. 2022).

Giving-up densities

To investigate habitat preference and perceived risk, GUD experiments were run three times each year roughly every two weeks between late June and end of July. We placed depletable food patches across the site in a 10 x 10 m grid (Appendix: Figure S2.1). Food patches consisted of a clear plastic saucer (36 cm diameter; Vigoro Chicago, Illinois, USA) filled with 2 liters of Cemex 30 mesh playbox sand and 5 g of millet (*Pennisetum glaucum;* a low-quality, but still avidly consumed food source; Brown 1988). Each year, roughly 100 plates were deployed to establish a permanent grid for each summer (2019 = 98 plates, 2020 = 106 plates). Plate location was consistent within a year; however, in 2020, we added a few plates to cover more space along some edges of the study site (Appendix: Figure S2.1).

Millet was evenly distributed and mixed throughout the sand and a few more highly preferred black oil sunflower seeds were placed on top of each plate as an initial lure. Plates were set out in the morning (0800 h) then collected at noon (1200 h) to capture this species' primary foraging time at our study site. During the experiment, observers sat at select locations (Appendix: Figure S2.1) and silently watched specific plates to note when individually marked ground squirrel(s) visited the plate and how long they foraged at the plate, if at all. We also noted if heterospecifics other than ground squirrels foraged at the plate. While most foraging visits were by ground squirrels, songbirds (e.g., oak titmouse [*Baeolophus inornatus*], scrub jays [*Aphelooma californica*]*),* American crow (*Corvus brachyrhynchos*), and tree squirrels (*Sciurus niger*) occasionally foraged at the plates. Because non-target visitors could contribute to GUDs (Gaynor et al. 2019) we included this co-variate in the analysis (hereafter 'non-target forager').

At the end of each experimental trial, the remaining millet was carefully sieved from the sand using a stainless-steel mesh sifting pan, and weighed using an Ohaus scale (± 0.001 g).

We focused on three outcomes for this experiment: (1) proportion of millet remaining (GUD), (2) number of unique foragers who visited the plates and (3) average time a forager spent on each plate during the four-hour experiment.

Squirrel density

As the proximity of other squirrels might have a strong influence on the GUDs, we estimated the local density of squirrels at the location of each plate. For each trial, we used the spatial data of all squirrels combined across a two-week period prior to the trial and calculated the utilization distribution (UD) using a kernel density estimation (grid size = 5 m). We then mapped the plate locations onto the UDs and calculated the local squirrel density for each plate as the UD of the nearest point on the UDs grid. We calculated overall squirrel density at each location instead of calculating the UD for each squirrel separately and then combining the UDs because roughly a third of the observed squirrels were recorded only rarely (≤ 5 times) and would have had to be excluded when calculating individual UDs.

Microhabitat

We assessed microhabitat features by taking a series of photographs at each plate used in the GUD experiment. We first constructed a quadrat (83.5 cm x 98 cm) which consisted of 36 (6 x 6) squares using PVC pipes. We then took photos from above the grid to generate a vegetation index to create a composite numerical score for each quadrat (dirt = 0, leaf litter = 0.5, living vegetation = 1; hereafter ‘ground cover’). In addition, photos of tree cover were taken from the ground with an overlaid grid and used to assign the proportion of tree coverage for each plate location (0 for open sky, 1 for tree vegetation; hereafter ‘sky cover’). All sky photos were quantified using a similar scoring system for each of the 36 cells within each quadrat. Lastly, we measured the distance to nearest burrow from each plate (Ortiz-Jimenez et al. 2022).

Statistical analysis

Analysis was conducted in R version 4.1.1 (R Core Team 2021). To investigate interannual differences in the proportion of millet remaining, local squirrel density, and visitor types, we conducted Mann-Whitney U tests due to unequal sample sizes between the years. We assumed significance when alpha was less than, or equal to, 0.05. Given our interest in the differences between the two years, we treated results from the pre-COVID and COVID year separately in our subsequent statistical modeling.

Structural equation modeling (SEM) conceptual framework

To analyze direct and indirect relationships between multiple predictor variables and our three main outcome variables, we implemented a Structural Equation Modelling (SEM) approach (see Figure 2.1). SEMs are a widely recognized tool for exploring causal relationships among variables and are particularly powerful in naturalistic settings that include observation measures (Iriondo et al. 2003) and colinear predictor variables (Graham 2003). A major goal of the current study was to understand variation in GUDs (amount of food remaining), where less food remaining reflects less fear of foraging at a particular experimental plate. GUDs depend on the number of foragers and mean time per visit, but also on individual feeding rates. Although we did not measure feeding rates or physiological fear directly, our SEM approach allowed us to assess these via direct impacts of predictor variables on GUDs beyond effects of the predictor variables on the number of foragers and mean time per visit on GUDs. We predicted that higher local squirrel density should reduce GUDs at a given patch by increasing the number of foragers visiting that patch, and if higher local density makes squirrels feel safer, that could result in longer mean times per visit and higher feeding rates (seeds eaten per second) during visits. In the SEM, the direct effect on GUDs is captured by the arrow going directly from a given factor to the GUD, while indirect effects can come through several multi-arrow, indirect pathways. For example, if squirrels fear humans and dogs, then humans and dogs can affect squirrel GUDs indirectly by reducing local squirrel density, number of unique squirrel visitors, and time per visit and directly by influencing intake rates by squirrels while visiting a given patch. Humans can also indirectly affect squirrel GUDs, by influencing the spatial pattern of rattlesnake or raptor activity that, in turn, can affect local squirrel density, the number of squirrels visiting a patch, average time per visit, and intake rates while in the patch. We predicted that habitat characteristics such as distance to refuge and habitat structure while out of refuge (e.g., ground cover, sky cover), predator activity, and the activity of humans (and dogs) may also affect GUDs via multiple direct and indirect pathways that are summarized in Figure 2.1.

Statistical implementation of SEMs

We implemented piecewise SEMs using the package piecewiseSEM (Lefcheck 2016) to investigate direct and indirect relationships among factors (Santillán et al. 2020). Prior to constructing our SEM, we investigated correlations between our variables. Because we uncovered high correlations between human activity and dog activity for both years (2019: r = 0.85; 2020: r = 0.98), we combined them into one composite variable (hereafter as ‘human & dog activity’). We constructed a fully saturated *a priori* model (Figure 2.1) which explored the causal relationship between giving-up density, numbers of unique foragers, average time a forager spent at a plate (henceforth ‘mean time per visit’), natural predator activity, microhabitat variables, anthropogenic variables, and our control for non-target foragers (recorded binary [0/1] if a non-target forager went to the plate during a trial). This saturated model included the maximum number of biologically plausible relationships (henceforth ‘paths’) between variables of interest (Antiqueira et al. 2020, Garrido et al. 2022) specified by the lmer() and glmer() function from the R package *lme4* (Bates et al. 2015) with ‘plate ID’ added as a random effect. Prior to the analysis, all variables were standardized. We applied the arcsine transformation to two dependent variables (proportion of millet remaining, local squirrel density) and square root transformations to activity measures for rattlesnakes and raptor to meet assumptions of normality.

We then used Shipley’s test of d-separation to identify non-significant paths and removed those based on the condition that it also lowered the BIC of the SEM. Our final models were selected based on the lowest BIC (Lin et al. 2017) and goodness of fit test (Appendix: Table S2.1, S2.2). We tested the goodness of fit for the models by a Fisher’s C test, which indicates a good model of fit if $P > 0.05$ (Shipley 2009). We then calculated the indirect effect of variables on our three variables of interest (GUD, number of unique foragers, and mean time per visit) by multiplying the direct effects of the connected paths (Example: Path description → $X * Y = Z$). We summed the direct and indirect effects to quantify the net effect of each variable on our outcome variables (Table 2.1, Appendix: Table S2.3, S2.4).

Results

Overall, we observed a total of 241 individual squirrels during experimental trials. Of these individuals, 106 squirrels (43% present at trials) visited plates in both years. The amount of remaining millet at the end of each trial was comparable between years (Mann-Whitney U-test: W = 50626, P = 0.08), ranging from 0.004 g to 5.06 g in 2019 (mean ± SE: 2.31 ± 0.10 g) and 0.11 g to 4.94 g in 2020 (2.20 ± 0.10 g). On average (±SE), 2.3 ± 0.17 unique foragers were observed at each plate in 2019 (median = 1, range: 0 to 19 individuals) and 2.1 ± 0.11 unique foragers in 2020 (median = 2, range: 0 to 9 individuals), numbers that were also comparable between years (W= 45120, P = 0.448). Interestingly, however, although each visitor only spent an average of 1.6 ± 0.10 minutes on the plates in 2019 (median = 1.45, range: 0 to 10.2 min), foragers remained on plates for significantly longer (2.4 ± 0.15 minutes) in 2020 (median = 2, range: 0 to 22 min; W = 37903, P = <0.001).

Figure 2.2 shows the spatial distribution of activity for humans & dogs, predators, and squirrels on a north-south gradient. Figure 2.3 shows the path diagrams summarizing the full set of significant relationships among independent and dependent variables. The direct, indirect, and net effects of various factors on GUDs are shown in Table 2.1.

Spatial distribution of humans, predators, and squirrel activity

Our study revealed several major distinctions between the pre-COVID (2019) and COVID (2020) years. First, the spatial distribution and variation in visits by humans & dogs and raptors differed between years (Figure 2.2B). In particular, in 2020, human & dog activity was more concentrated in the most southern section of the study area, as humans mainly entered the area to use the restroom, wash their hands, or offer their dogs water at a water fountain before setting off for a hike. In contrast, human & dog activity was more evenly distributed across the site in 2019. While the southernmost sections still had the highest use, visitors stayed longer inside the picnic area per visit in 2019 compared to 2020 (Figure 2.2A). Second, we found a significant difference in local squirrel density between years; the local density of squirrels per plate was higher in 2020 than in 2019 ($W = 33895$, $P < 0.001$, Figure 2.2B). Despite these differences in the spatial distribution of visitors, the overall hourly rate of visits to the study site for each visitor type (i.e., humans & dogs, rattlesnakes, raptors) did not significantly differ between years (human & dog: $W = 47520$, $P = 0.723$; rattlesnakes: $W = 44744$, $P = 0.2702$; raptors: $W = 45504$, $P = 0.549$).

Effects of squirrel density, and visits to trays on GUDs

With regard to factors affecting GUDs, as expected, there was less food remaining in plates that were visited by more unique squirrels and where squirrels exhibited longer mean times per visit (Figure 2.3). While biologically this is expected, we found that the overall effect of both variables was stronger in the COVID year (2020, net effect: number of unique foragers = -0.412, mean time per visit = -0.515) than in 2019 (net effect: number of unique foragers = -0.146, mean time per visit = -0.223). For both years, as expected, we saw an overall positive correlation between local squirrel density and number of unique foragers, although the strength of the net effect was slightly weaker in 2020 compared to 2019. Further, in the non-COVID year (2019) squirrels spent more time on plates in areas of higher local squirrel density, which we did not find in 2020.

Beyond the indirect effect of local squirrel density on seeds consumed via effects from squirrel density on number of foragers to a plate and average visit duration in 2019, squirrel density also had a direct negative effect on GUDs (i.e., less food remained in plates with high local squirrel density). That is, squirrels in high density areas ate faster during visits at a plate. However, this trend did not continue in the COVID year (2020), when squirrel density only influenced GUDs indirectly and minimally. Still, squirrel density had an overall negative effect on GUDs in both years (net effect: 2019 = -0.442, 2020 = -0.086).

Non-target foragers visited 7% of plates in 2019 and 25% of plates in 2020 on at least one occasion for any of the three trials within a year. However, these non-target foragers did not significantly have a direct impact on the final GUDs in either year. Instead, we found non-target foragers indirectly influenced GUDs through the number of unique squirrel foragers in our COVID year only, with squirrels more likely to visit plates that non-target foragers had also visited. This effect was quite small however (net effect: -0.029); thus, non-target visitors had almost no effect in our overall study.

Human, predator, and habitat effects on GUDs

2019: Pre-COVID

Human & dog activity directly reduced GUDs, suggesting squirrels were less fearful while foraging in areas with increased human & dog presence (e.g., Section 1 of Figure 2.2). Although human & dog activity was associated with lower local squirrel density (i.e., squirrels avoided areas of higher human & dog activity), human & dog activity had an overall negative effect on GUDs via multiple pathways; less food remained in plates with higher human & dog activity (net effect: -0.183), suggesting reduced fear in these regions.

In terms of predators, rattlesnake activity was positively correlated with human & dog activity and squirrel density (Figure 2.3A). Via both of these pathways, rattlesnake activity was also negatively correlated with GUDs (net effect: -0.129), presumably because rattlesnakes reside in areas of high local squirrel density. Raptor activity influenced mean time per visit where squirrels spent less time foraging on plates with high raptor presence; however, the overall effect on GUDs was weak (net effect: 0.031).

Lastly, the habitat feature of distance to burrow had the strongest effect on GUDs both directly and indirectly (net effect: 0.353). Plates farther from burrow refuge had more food remaining (i.e., fear increased with distance from refuge) because they received fewer visits, with shorter average time per visit, and lower foraging rate while at the tray. Other habitat effects such as increased sky cover and ground cover were also associated with more food remaining in plates; however, these effects were weak compared to our other variables of interest.

2020: A COVID year

Interestingly, in 2020, we found human & dog activity to have a much weaker overall effect on GUDs and other variables compared to the previous pre-COVID year. Human & dog activity did not directly influence foraging rate (i.e., GUDs), and while the indirect effect continued to be less food remaining in plates with higher human & dog activity, this effect was weak (indirect and net effect = -0.023).

With regard to predators, we continued to see a positive correlation between rattlesnake activity and human & dog activity along with the positive relationship with local squirrel density, resulting in lower GUDs (i.e., less food remaining reflecting less fear) in 2020. However, the strength of these effects was weaker than the previous year; in 2020, the net rattlesnake effect was only -0.016. The most notable change we found in 2020 was the increase in the overall effect of raptor activity on GUDs (net effect: 0.145). Squirrels actively avoided areas with higher raptor activity (i.e., lower local squirrel density) and had shorter mean visitation times where raptor activity was higher, which resulted in more food remaining in plates. We also found a negative relationship between raptor activity and human & dog activity, in that there were fewer raptors present in areas of high human & dog activity. Thus, in 2020, raptors avoided the high human & dog areas (Section 1, Figure 2.2), and squirrels were more fearful in the areas where raptors resided (i.e., Section 5-7, Figure 2.2).

With the increase of raptor activity in 2020, we also found habitat effects to play a larger role than the previous year. Distance to burrow continued to have a strong indirect influence on GUDs by having fewer foragers and shorter visitation times at plates further from burrow refuge. However, in 2020, unlike in 2019, distance to burrow no longer directly influenced GUDs. While the overall effect of distance to burrow was weaker than the previous year, it still had one of the strongest effects on GUDs (net effect: 0.207). We saw a similar trend with other habitat features, with squirrels leaving more food in plates (i.e., more fearful) in areas with more ground cover and less sky cover. High ground cover now had a strong overall positive effect on GUDs (net effect: 0.301); i.e., in 2020, squirrels were more fearful in areas with more ground cover. Although there were more squirrels in areas with high ground cover, high ground cover strongly reduced the number of visitors to trays (Appendix: Table S2.3) and squirrels foraged at a lower rate when in sites with high ground cover (direct effect: 0.270). Higher sky cover did not significantly influence the number of squirrel visitors or time per visit but tended to increase squirrel foraging rate while at trays (direct effect: -0.144).

Discussion

Overall, we found that changes in human behavior and space use due to pandemic disruption had significant impacts on ground squirrel risk perception. Between a COVID and non-COVID year, we found that different factors altered how ground squirrels navigated the landscape. These ranged from avoidance of an area altogether to subtle changes in number of foragers or time spent foraging at a patch. While GUDs alone did provide information about fearfulness across the landscape, our added measures of number of unique foragers, average time spent foraging at a patch, and feeding rate while at a patch provided finer scale details on the factors that influence fear in the California ground squirrel.

We saw similar rates of activity for all visitor types between both years; however, we found that a shift in visitor space use between years had significant impacts on risk-sensitive foraging. In 2019, the pre-COVID year, when human and dog activity was less concentrated in one area, squirrels were presumably less fearful (had lower GUDs) in areas of high human & dog activity. This fits the 'enemy of my enemy is my friend' idea seen in other systems (Leighton et al. 2010, Kuijper et al. 2015, Suraci et al. 2019, Caldwell and K. Klip 2022) where human presence can be beneficial for prey, perhaps by reducing predation risk from real predators. Importantly, however, our ability to partition direct and indirect pathways suggested that squirrels are not 'fearless' of humans, but rather exhibited a mix of higher versus lower fear of human & dog activity at different temporal scales. In 2019, on a weekly scale, squirrels showed a tendency to avoid areas with higher human & dog activity, but when squirrels used those areas, their foraging intake rate was significantly higher (i.e., lower GUDs, less fear). In contrast, in the COVID year, we did not see any direct relationship between human & dog activity and foraging rate even though overall human & dog activity was similar to the previous year. Perhaps because human & dog activity was strongly concentrated in one region of the study site, it had only a small effect on squirrel GUDs. Squirrels, surprisingly, did not tend to shift their movement patterns to avoid those areas, but showed a weak tendency in areas with higher human & dog activity to visit plates less frequently, and for shorter periods. These results suggest that beyond effects of overall human activity per se, the spatial concentration of human activity can play a key role in how humans impact prey landscapes of fear.

For both years we found raptor activity to be negatively correlated with human & dog activity; however, in 2020, the COVID year, when human & dog activity had little effect on squirrel GUDs, raptors had much stronger effects on squirrel GUDs than in 2019. We found that squirrels often avoided areas of higher raptor activity, but also expressed fear through shorter foraging times which significantly influenced GUDs. Overall, in the pre-COVID year, the impact of raptors on GUDs was weak, whereas in the COVID year, the impact of raptors on GUDs (i.e., fear of raptors) was much stronger. This occurred even though the overall activity of raptors did not differ between years, but conceivably reflected the change in the spatial pattern of raptor activity associated with the more concentrated use of space by humans and dogs in 2020.

With the shift in human & dog space use, we also found a change in the relative importance of habitat features used by squirrels to assess risk. In both years, squirrels' fear strongly and consistently increased the farther they were from refuge, an expected finding for this species (Ortiz-Jimenez et al. 2022). In the non-COVID year, distance to refuge was the strongest microhabitat factor which impacted forging rate both directly and indirectly. Distance to refuge also decreased local squirrel density which further decreased number of foragers to visit a plate above and beyond squirrel's avoidance of these areas. In 2020, distance to refuge did not affect local squirrel density, but did indirectly impact foraging rate through a decreased number of foragers at plates and via shorter visit durations. More strikingly, with the increase of fear of raptors in the COVID year, squirrels altered their response to variation in ground and sky cover. Compared to the non-COVID year, squirrels increased their foraging rate in areas with more sky cover from surrounding trees, suggesting they were less vigilant and more focused on foraging in these areas safe from raptors. Surprisingly, while local squirrel density was higher in areas of increased ground cover (i.e., squirrels did not avoid areas of high vegetation and leaf litter), they often chose not to forage in these areas in either year; however, this effect had a stronger impact on the landscape of fear in the COVID year.

We found a positive correlation between local squirrel density and the activity of the squirrel's other natural predator, the rattlesnake. This finding is consistent at the larger scale, with species abundances for ground squirrels and rattlesnakes co-varying across the state of California (Poran et al. 1987). Rattlesnakes also tended to have higher activity where humans & dogs also had higher activity. We do not suggest that squirrels are choosing to be near rattlesnakes but rather that both species may be utilizing refuge provided by humans & dogs since raptor species, including red-tailed hawks, are active predators of ground squirrels as well as rattlesnakes (Fitch et al. 1946).

In conclusion, we found that changes in human activity due to COVID-19 protocols had significant impacts on how free-living animals navigate and assess the landscape of fear. These findings contribute to growing evidence for how global shutdowns affect wildlife living in urban and semi-urban environments (Zellmer et al. 2020). Our experimental study importantly captures shifts in fear responses that help to address long-standing questions in urban ecology, extending previous findings about the effect of human presence on refuge use. For example, although globally animals have become increasingly nocturnal to avoid humans (Gaynor et al. 2018), COVID-19 lockdowns reversed these trends for birds, promoting a rapid increase in their daytime activity in Spain (Gordo et al. 2021). Globally, animal species responded quickly – and usually positively – to reductions in human presence associated with lockdowns (Bates et al.

2021). In particular, carnivore numbers and movements increased in urban areas during lockdowns (Silva-Rodríguez et al. 2021). In contrast, we show *increased fear* among small prey mammals associated with COVID-linked *reductions in human activity*. That is, although ground squirrels are not fearless of humans (e.g., shorter foraging bouts and avoidance of areas with high human activity), these prey animals were more fearful during lockdowns when they presumably lacked access to the spatial refuges from predators provided by humans. Importantly, however, our results suggest that how humans affect the squirrels' landscape of fear depends on a complex interplay between the spatial concentration of human (and dog) activity and responses of multiple predators mediated by multiple landscape features. Thus, our findings offer new insights into the varied ways that human presence – through direct and indirect effects within ecological communities – influence animal perception of safety and danger in a changing world.

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Table 2.1. Standardized direct, indirect, and net estimates of predictor variables on our outcome variable of giving up density in 2019 and 2020.

A)

Variable	**Standard estimate**		
	Direct	*Indirect*	*Net*
Mean time per visit	-0.130	-0.093	-0.223
Number of unique foragers	-0.146	n.s	-0.146
Squirrel density	-0.340	-0.105	-0.442
Human & dog activity	-0.260	0.076	-0.183
Rattlesnake activity	n.s	-0.129	-0.129
Bird of prey activity	n.s	0.031	0.031
Distance to burrow	0.178	0.175	0.353
Ground cover	n.s	0.056	0.056
Sky cover	n.s	0.084	0.084
Non-target forager	n.a	n.a	n.a

B)

Variable	**Standard estimate**		
	Direct	*Indirect*	*Net*
Mean time per visit	-0.330	-0.185	-0.515
Number of unique foragers	-0.412	n.s	-0.412
Squirrel density	n.s	-0.086	-0.086
Human & dog activity	n.s	-0.023	-0.023
Rattlesnake activity	n.s	-0.016	-0.016
Bird of prey activity	n.s	0.145	0.145
Distance to burrow	n.s	0.207	0.207
Ground cover	0.170	0.131	0.301
Sky cover	-0.144	n.s	-0.144
Non-target forager	n.s	-0.029	-0.029

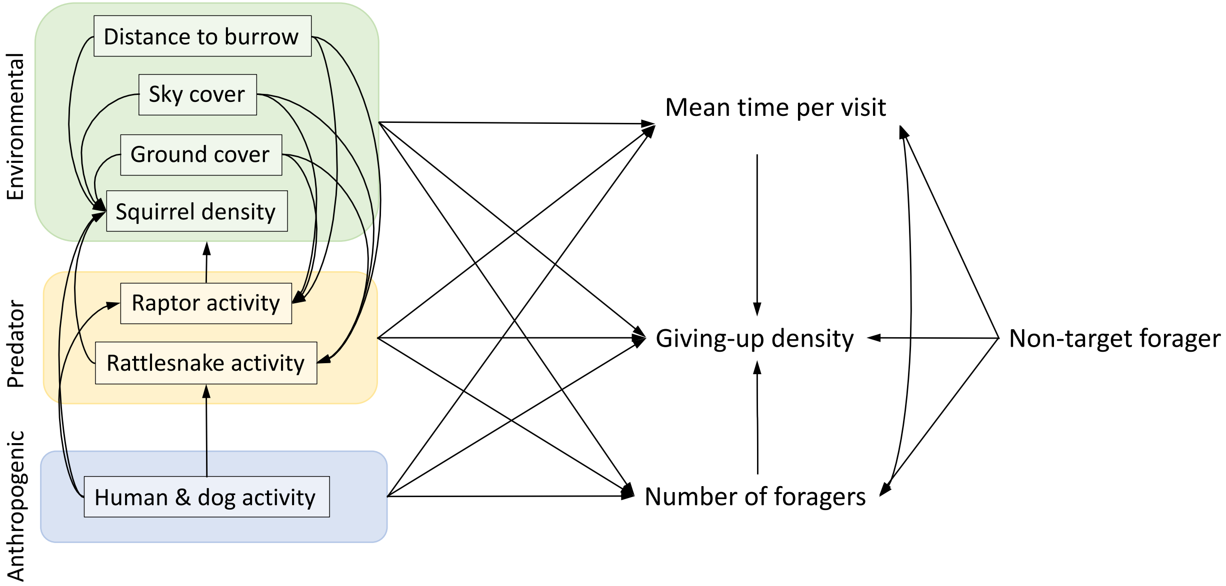
n.s., not significant; n.a., not applicable

Figure captions

Figure 2.1. *A priori* model of all variables included in the model and all biologically relevant paths.

Figure 2.2. a) Spatial map of study site with plate locations separated into 7 sections from north to south and b) Average activity from all visitor types (humans and dogs, rattlesnakes, and raptors) and average local squirrel density from plates in the associated sections from the spatial map. Error bars indicate standard error.

Figure 2.3. Final piecewise structural equation model (SEM) for a) 2019 and b) 2020. Each variable is shown in a box, with dependent variables shown with the marginal R^2 and conditional R^2 value. For both SEMs, arrows represent unidirectional relationships among the variables with solid lines representing positive effects and dashed lines representing negative effects. The number along each path (arrows) is the standardized estimate while the line thickness represents the significance strength with thicker lines being more significant.



Environmental
Predator
Anthropogenic
Distance to burrow
Sky cover
Ground cover
Squirrel density
Raptor activity
Rattlesnake activity
Human & dog activity
Mean time per visit
Giving-up density
Number of foragers
Non-target forager

Figure 2.1.

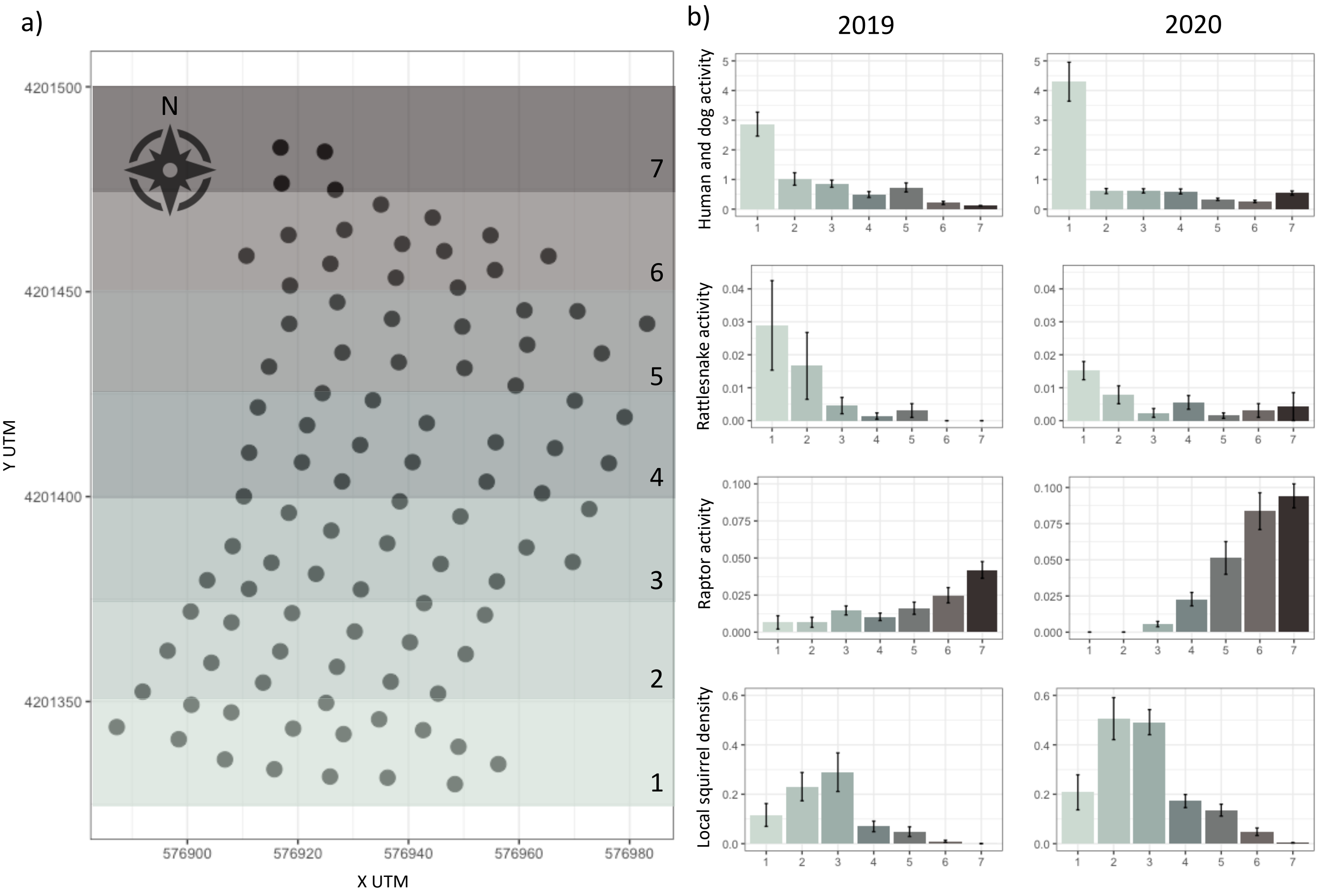

a)
b)
2019
2020
N
Y UTM
X UTM
4201500
4201450
4201400
4201350
576900
576920
576940
576960
576980
1
2
3
4
5
6
7
Human and dog activity
Rattlesnake activity
Raptor activity
Local squirrel density

Figure 2.2.

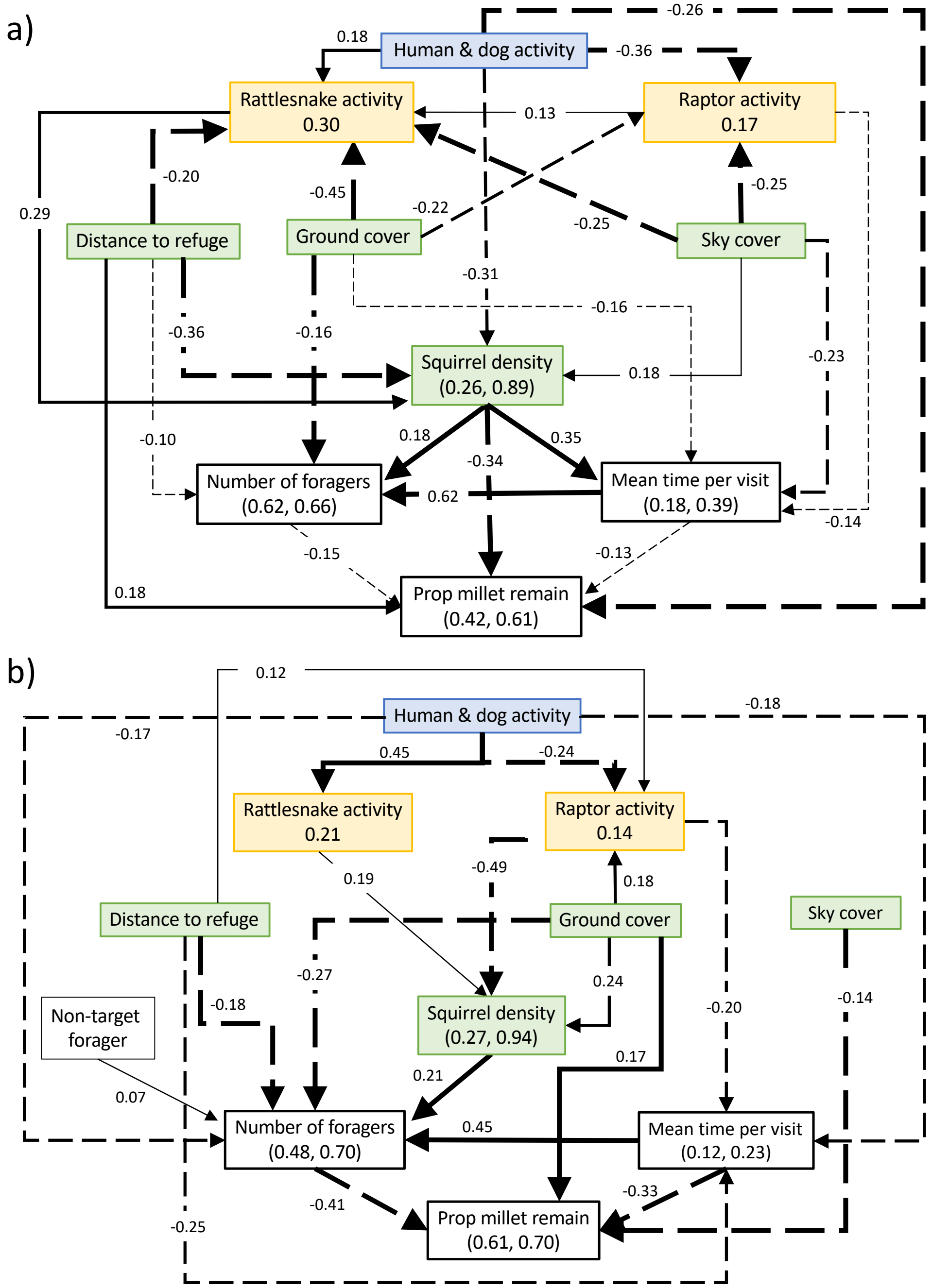

a)
0.18
Human & dog activity
-0.36
-0.26
Rattlesnake activity
0.30
0.13
Raptor activity
0.17
-0.20
0.29
-0.45
-0.22
-0.25
Distance to refuge
Ground cover
-0.25
Sky cover
-0.31
-0.16
-0.36
-0.16
-0.23
Squirrel density
(0.26, 0.89)
0.18
-0.10
0.18
-0.34
0.35
Number of foragers
(0.62, 0.66)
0.62
Mean time per visit
(0.18, 0.39)
-0.14
-0.15
-0.13
0.18
Prop millet remain
(0.42, 0.61)
b)
0.12
-0.18
Human & dog activity
-0.17
0.45
-0.24
Rattlesnake activity
0.21
Raptor activity
0.14
0.19
-0.49
0.18
Distance to refuge
Ground cover
Sky cover
-0.27
-0.18
0.24
-0.20
-0.14
Non-target
forager
Squirrel density
(0.27, 0.94)
0.17
0.21
0.07
Number of foragers
(0.48, 0.70)
0.45
Mean time per visit
(0.12, 0.23)
-0.33
-0.41
-0.25
Prop millet remain
(0.61, 0.70)

Figure 2.3.

Appendix

Table S2.1. List of each path removed from *a priori* SEM and the associated degrees of freedom (df), Fisher's C, AIC, BIC and P-value change. The final model selected is shown in bolded text, chosen based on lowest BIC value.

Round Number	df	Fischer's C	AIC	BIC	P-value	Path removed
1	10	215.947	327.947	534.227	0	
2	8	45.672	159.672	369.636	0	Add mean time per visit to number of unique foragers
3	6	36.136	152.136	365.784	0	Add raptor activity to rattlesnake activity
4	8	36.229	150.229	360.193	0	Remove sky cover from proportion millet remain
5	10	36.360	148.360	354.640	0	Remove rattlesnake activity from proportion millet remaining
6	12	36.595	146.595	349.192	0	Remove distance from nearest burrow from raptor activity
7	14	36.901	144.901	343.814	0.001	Remove human & dog activity from number of unique foragers
8	16	38.042	144.042	339.272	0.001	Remove raptor activity from number of unique foragers
9	18	39.302	143.302	334.848	0.003	Remove non-target forager from percent millet remain
10	20	40.641	142.641	330.504	0.004	Remove non-target forager from mean time per visit
11	22	42.079	142.079	326.258	0.006	Remove human & dog activity from mean time per visit
12	24	43.204	141.204	321.699	0.009	Remove rattlesnake activity from mean time per visit
13	26	45.377	141.377	318.189	0.011	*Remove rattlesnake activity from number of unique foragers*
14	28	47.445	141.445	314.573	0.012	Remove sky cover from squirrel density
15	30	49.965	141.965	311.410	0.013	Remove ground cover from proportion millet remaining
16	20	11.765	101.765	267.526	0.924	Remove non-target forager from number of unique foragers
17	22	14.349	102.349	264.427	0.889	Remove bop from proportion millet remaining
18	24	17.84	103.84	262.234	0.811	Remove sky cover from number of unique foragers
19	26	23.123	107.123	261.833	0.626	Remove raptor activity from squirrel density
20	28	28.089	110.089	261.116	0.46	Remove distance from nearest burrow from mean time per visit
21	**28**	**27.387**	**109.387**	**260.414**	**0.497**	**Remove ground cover from squirrel density**

Table S2.2. List of each path removed from *a priori* SEM and the associated degrees of freedom (df), Fisher’s C, AIC, BIC and P-value change. The final model selected is shown in bolded text, chosen based on lowest BIC value.

Round Number	df	Fischer's C	AIC	BIC	P-value	Path removed
1	10	126.706	238.706	449.381	0	
2	8	10.005	124.005	338.442	0.265	Add foraging mean to number of unique foragers
3	10	10.375	122.375	333.05	0.408	Remove ground cover from rattlesnake activity
4	12	10.896	120.896	327.809	0.538	Remove non-target forager from mean time per visit
5	14	11.507	119.507	322.658	0.646	Remove rattlesnake activity from proportion millet remain
6	16	12.313	118.313	317.702	0.722	Remove rattlesnake activity from number of unique foragers
7	18	13.239	117.239	312.866	0.777	Remove distance dearest burrow from proportion millet remain
8	20	14.42	116.42	308.285	0.809	Remove distance from nearest burrow from squirrel density
9	22	16.183	116.183	304.286	0.807	Remove rattlesnake activity from mean time per visit
10	24	18.063	116.063	300.404	0.800	Remove squirrel density from proportion millet remain
11	26	19.796	115.796	*296.374*	*0.801*	*Remove ground cover from mean time per visit*
12	28	22.705	116.705	293.521	0.748	Remove sky cover from squirrel density
13	30	25.669	117.669	290.723	0.642	Remove non-target forager from percent millet remain
14	32	29.814	119.814	289.106	0.578	Remove squirrel density from mean time per visit
15	34	33.399	121.399	286.929	0.497	Remove sky cover from mean time per visit
16	36	36.650	122.650	284.418	0.439	Remove sky cover from raptor activity
17	38	40.827	124.827	282.833	0.347	Remove distance from nearest burrow from rattlesnake activity
18	40	45.052	127.052	281.296	0.269	Remove sky cover from rattlesnake activity
19	42	50.030	130.03	280.512	0.185	Remove human & dog activity from squirrel density
20	44	54.962	132.962	279.682	0.124	Remove sky cover from number of unique foragers
21	46	57.579	133.579	276.537	0.118	Remove raptor activity from number of unique foragers
22	48	62.262	136.262	275.458	0.081	Remove raptor activity from proportion millet remain
23	**50**	**65.233**	**137.233**	**272.667**	**0.073**	**Remove human activity from proportion millet remain**

Table S2.3. Standardized direct, indirect, and net effects of variables on number of unique foragers in A) 2019 and B) 2020.

A)

Variable	**Standard estimate**		
	Direct	*Indirect*	*Net*
Mean time per visit	0.625	n.s	0.625
Squirrel density	0.180	0.217	0.397
Human & dog activity	n.s	0.028	0.028
Rattlesnake activity	n.s	0.115	0.115
Raptor activity	n.s	-0.072	-0.072
Distance to burrow	-0.100	-0.143	-0.238
Ground cover	-0.160	-0.080	-0.240
Sky cover	n.s	-0.082	-0.082
Non-target forager	n.s	n.s	n.s

B)

Variable	**Standard estimate**		
	Direct	*Indirect*	*Net*
Mean time per visit	0.447	n.s	0.447
Squirrel density	0.209	n.s	0.209
Human & dog activity	-0.174	0.064	-0.110
Rattlesnake activity	n.s	0.040	0.040
Raptor activity	n.s	-0.193	-0.193
Distance to burrow	-0.185	-0.136	-0.321
Ground cover	-0.270	0.016	-0.254
Sky cover	n.s	n.s	n.s
Non-target forager	0.070	n.s	0.070

n.s., not significant

Table S2.4. Standardized direct, indirect, and net effects of variables average time a forager spent on a plate (mean time per visit) in A) 2019 and B) 2020.

A)

Variable	**Standard estimate**		
	Direct	*Indirect*	*Net*
Squirrel density	0.353	n.s	0.353
Human & dog activity	n.s	0.064	0.064
Rattlesnake activity	n.s	0.102	0.102
Raptor activity	-0.140	0.013	-0.125
Distance to burrow	n.s	-0.126	-0.126
Ground cover	-0.160	0.028	-0.136
Sky cover	-0.230	0.006	-0.229
Non-target forager	n.s	n.s	n.s

B)

Variable	**Standard estimate**		
	Direct	*Indirect*	*Net*
Squirrel density	n.s	n.s	n.s
Human & dog activity	-0.180	0.048	-0.131
Rattlesnake activity	n.s	n.s	n.s
Raptor activity	-0.200	n.s	-0.200
Distance to burrow	-0.250	-0.024	-0.275
Ground cover	n.s	-0.036	-0.036
Sky cover	n.s	n.s	n.s
Non-target forager	n.s	n.s	n.s

n.s., not significant

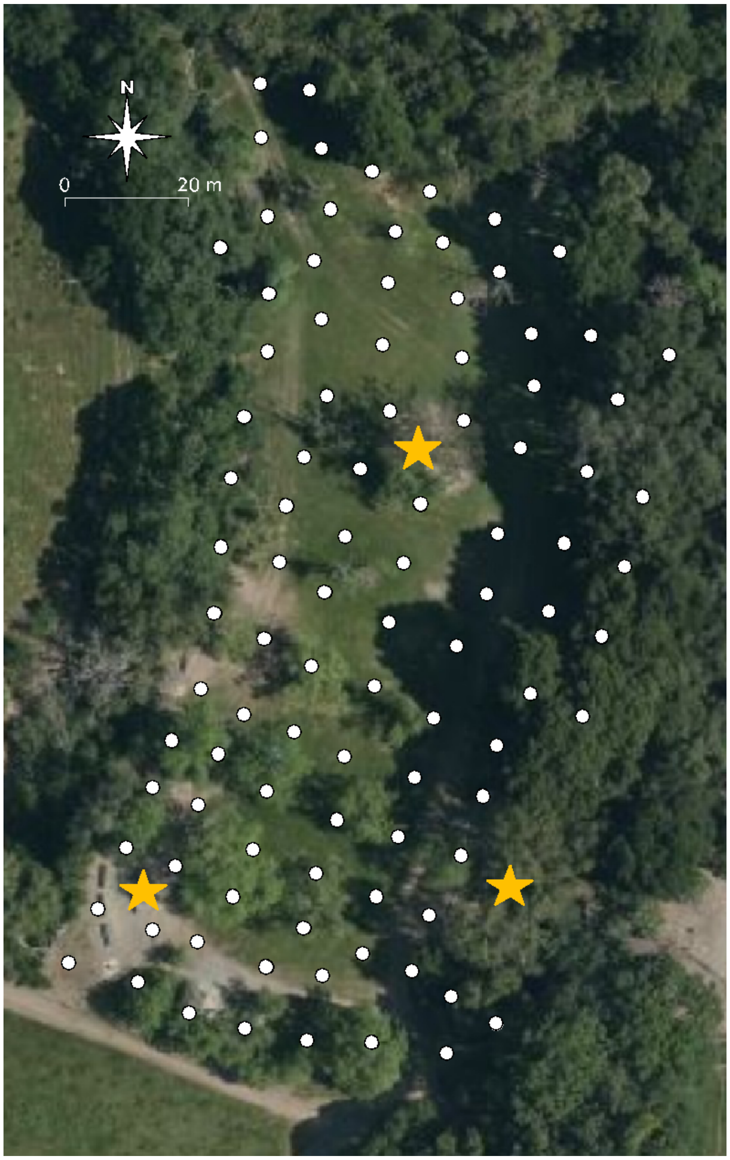


Figure S2.1. Aerial image of study site at Briones Regional Park, Contra Costa County, CA. White dots represent plate locations. Gold stars represent locations where observers quietly sit on picnic benches during experiment to record ground squirrel visitations at each individual plate.

Human disturbance is associated with increased apparent survival in a free-living ground squirrel

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Abstract

Human presence in natural environments has been shown to influence wildlife behavior and survival. While human disturbance is generally associated with negative impacts on wildlife, recent studies suggest that in some cases, humans may provide vulnerable animals safety from predators. To investigate the effect of human disturbance on mortality and site fidelity, we conducted a long-term study on a semi-urban population of California ground squirrels (*Otospermophilus beecheyi*). Using capture-mark recapture analysis, we investigated the effects of sex, age, body condition, personality, and flea load on apparent survival (true survival and permanent emigration) within both high and low human-disturbed environments. Our findings revealed that human disturbance increased apparent survival rates in male ground squirrels but not in females. Instead, for females, we found an interaction between human disturbance and age, where young female ground squirrels had slightly higher apparent survival rates in areas of higher human disturbance, whereas squirrels aged three and older showed the opposite trend. Among males, human disturbance and age were the strongest predictors of apparent survival, with juvenile males in areas with low human disturbance exhibiting the lowest apparent survival rates. Additionally, behavioral reactivity in the trap and during handling played a role in apparent survival, with the effects dependent on sex and age. This long-term study provides insights into the complex relationship between human disturbance and wildlife survival, highlighting the potential positive role humans can play in certain ecological systems.

Introduction

Across the world, human activity and infrastructure have rapidly expanded worldwide causing anthropogenic disturbances that affect wildlife behavior (Gaynor et al. 2018, Kunc and Schmidt 2019, Turner et al. 2020), and survival (López-Roig and Serra-Cobo 2014, Gibson et al. 2018, Matias et al. 2022). For example, in a coastline bird, mortality rates were significantly higher in areas of increased human disturbance, likely due to degradation of the coastal habitat and increased human foot traffic destroying nests (Gibson et al. 2018). Human disturbance has historically been assumed to have a detrimental impact on wildlife survival. Indeed, humans contribute to more than half of the mortality among medium and large-sized North American mammals (Collins and Kays 2011), attributed primarily to hunting and vehicle collisions, both of which are positively associated with human development. Recently, however, researchers have found that in natural landscapes, humans may provide a benefit to some species, particularly small mammals, by providing refuge from natural predators (Lamichhane et al., 2023; Ortiz-Jimenez et al., in prep; Suraci, Clinchy, Zanette, & Wilmers, 2019). Thus, exploring the potential impact of humans on mortality and habitat selection in small mammals should reveal the extent that humans may also shape the traits of small mammals and, more broadly, contribute to our understanding of rapid plastic or evolutionary shifts in the behavior and morphology of animals in response to human-induced change (Sih 2013; Caspi et al. 2023).

Apparent survival is the product of true survival plus losses associated with permanent emigration (i.e., dispersal; Nicholson, Bejder, Allen, Krtzen, & Pollock, 2012; Wild et al., 2019). A myriad of factors has been found to influence an individual's survival in human-dominated landscapes. Most importantly, life-history and behavioral differences between the sexes and across ages can influence how individuals interact with humans and human-altered habitats

(Promislow and Harvey 1990), and thus, impact their fitness in human-disturbed environments (Stevens et al. 2023). For example, female Andean condors (*Vultur gryphus*) have strong habitat-selection preferences, scavenging most often in humanized areas, whereas males avoid these habitats. This sex-dependent preference differentially exposes females to anthropogenic dangers (e.g., roads, cars, cable lines) leading to higher mortality rates for females than their male counterparts (Lambertucci et al. 2012).

Mortality risk can also vary with the age or condition of animals in human-altered habitats. Juveniles are typically more vulnerable than adults and are likely to exhibit higher mortality rates from predators (Caughley 1966, Clutton-Brock et al. 1985, Sullivan 1989, Collins and Kays 2011). In addition, in order to gain mass quickly, juveniles often take greater risks to feed. Conversely, as individuals age, they can become susceptible to injury and disease, which may be exacerbated in areas with increased anthropogenic disturbance. These age-related costs may be associated with body condition. While the relationship between body condition and mortality can be complicated (Milenkaya et al. 2015, Geissinger et al. 2023), generally, individuals in poorer body condition may have less access to resources or face higher predation pressures (Cowan et al. 1996, Gustafsson et al. 2010).

Personality, defined as consistent individual differences in behavior, may also impact the survival and habitat selection in human-disturbed environments (Cote et al. 2010). Several studies have found links between personality and traits such as dispersal (Cote et al. 2010, Chapple et al. 2012), movement (Spiegel et al. 2017, Michelangeli et al. 2022), habitat use (Wilson et al. 2020, Payne et al. 2022), and survival (Piquet et al. 2018, Turner et al. 2020, Moiron et al. 2020). For example, animals living in urban habitats tend to be bolder, more exploratory, and more aggressive. Whereas boldness may be advantageous for obtaining high quality resources, it may also increase chance of injury or death (Réale et al. 2007, Miranda et al. 2013). Nonetheless, in nature, survival tends to be higher for individuals with bold behavioral types (Moiron et al. 2020).Thus, we expect an individual's personality to interact with other key traits to impact apparent survival in human-altered environments.

Phenotype-dependent dispersal and mortality, both of which are subject to selection in human-altered environments, are fundamental ecological processes that shape adaption and metapopulation dynamics (Cote et al. 2010). Mammalian dispersal, defined as a complete and permanent emigration from an individual's home range (Holekamp 1984), typically involves juvenile males leaving their natal site to settle elsewhere to breed (Greenwood 1980, Pusey 1987). Because dispersal is often dangerous (Stamps 2001) it can result in decreased survival on the dispersing sex at predictable times across an individual's life (Weldy et al. 2022). In altered environments, humans may disrupt dispersal via habitat fragmentation (Smith and Batzli 2006, Baguette and Van Dyck 2007) or promote site fidelity (Murray et al. 2021); these effects may further interact with individual-based attributes of animals, such as their personality. Personality, defined as consistent individual differences in behavior, may also impact the survival, dispersal, and habitat selection in human-disturbed environments (Cote et al. 2010).

Lastly, parasites often have detrimental effects on survival (Monticelli and Ramos 2012), but in some cases, positively co-vary with factors that enhance survival, such as group size (Hillegass et al. 2008). The complex relationships between parasite loads and survival may be further influenced by human factors. For example, animals living in urban areas tend to have higher parasite loads (Murray et al., 2019; Thawley et al., 2019). In semi-urban parks, however, upkeep of the surrounding vegetation in areas of increased human foot traffic may be beneficial in keeping parasite numbers low (Smith et al. 2021). This may, in turn, benefit animals residing in these areas. Further, individuals have been found to differ consistently in parasite loads (Payne et al. 2020, Smith et al. 2021) associated with host sex (Krasnov, Morand, Hawlena, Khokhlova, & Shenbrot, 2005), age (Krasnov, Burdelova, Khokhlova, Shenbrot, & Degen, 2005) and personality (Sih et al. 2018). Yet, the extent to which parasite loads influence survival per se requires addition study.

While many studies have looked at how these factors have individually influenced apparent and true survival, very few have explored them in combination. Even fewer studies have long-term data to investigate the relative roles of these factors on survival and emigration in human-dominated environments. Long-term data sets are essential for evaluating potential population-level impacts of novel threats, such as human disturbance (Monticelli and Ramos 2012, López-Roig and Serra-Cobo 2014). In sum, long-term data sets of multiple individual-level and ecological factors can provide a better understanding of why certain individuals thrive in environments with increased human presence while others do not.

For this study, we used 9 consecutive years of individual-based data to investigate the sex and age-specific effects of spatial variation in human disturbance on apparent survival in the California ground squirrel (*Otospermophilus beecheyi*). We explored these patterns while investigating the effects of body condition, personality, and ectoparasite loads on apparent survival. California ground squirrels are a major prey species for many predators (Smith et al. 2016). These ecosystem engineers construct underground burrows that provide refuge for themselves and other species (Augustine, Smith, Davidson, & Stapp, in press.; McCullough Hennessy et al., 2016), contributing to ecosystem health (Swaisgood et al. 2019).

Mortality and dispersal in California ground squirrels is likely shaped by an individual's sex, age, body condition, personality, and flea loads. Although data on California ground squirrel movement ecology is limited, they likely adhere to the typical mammalian pattern of dispersal by juvenile males. For example, male but not female Belding's ground squirrels (*Urocitellus beldingi*) of sufficient body condition typically disperse after their first year (Holekamp 1984). Thus, we predicted sex-biased dispersal to decrease apparent survival in young males but expected similar rates of apparent survival for both sexes thereafter. These effects are likely also influenced by body condition. Whereas adults are generally able to cope with rattlesnake venom, venom resistance decreases with poor adult body condition (Holding et al. 2020) and only juveniles of sufficient body condition may survive rattlesnake bites (Poran et al. 1987). Thus, we expect increased apparent survival for those in the best condition. Ground squirrels have also been shown to exhibit consistent individual differences in behavior, including antipredator behavior (Ortiz-Jimenez et al. 2022), and we predict that as in other small mammals, behavioral type variation might explain variation in apparent survival, particularly with respect to human disturbance. California ground squirrels in areas with increased human presence respond boldly to human approach (Ortiz-Jimenez et al. 2022) and encounter limited natural predators (Ortiz-Jimenez et al., in prep). Finally, although flea loads on host squirrels generally increase with levels of human disturbance (Patz et al. 2000, Hubbart et al. 2011, Durden et al. 2019, Smith et al. 2021), the downstream effects of fleas on apparent survival are unclear and may be positive or negative.

Methods

We conducted capture-mark-recapture (CMR) surveys at Briones Regional Park in Contra Costa County, California, USA (Latitude: 37.93 North, Longitude: 122.13 West, Elevation: 319 m above mean sea level) from 2013 to 2021. The habitat consists primarily of open oak savannah interspersed with heavily vegetated riparian corridors. Our main study site is an established picnic area which typically has moderate levels of human activity that varies spatially across the site (Figure 3.1; Ortiz-Jimenez, Michelangeli, Pendleton, Sih, & Smith, 2022). We quantified fine-scale spatial variation in human activity levels following methods described in detail in Ortiz-Jimenez et al. (2022). The spatial distribution of human visitors tends to be clustered around amenities (e.g., a bathroom and water fountain) towards the southern end of the site which allowed us to split the site into two zones of high versus low human disturbance based on the median of disturbance for each year (Figure 3.1b).

Since May of 2013, individual ground squirrels within our study population were captured using Tomahawk traps (Tomahawk Live Trap Co., Hazelhurst, Wisconsin) baited with sunflower seeds and peanut butter. Trapping was conducted every 2 weeks from early May to late July. This is the time of year when juveniles are recruited into the population, mortality from rattlesnake predators or food limitation is expected to be highest, and individuals are most active aboveground for trapping. Traps were opened during the daytime and each trap was shaded with cardboard and frequently checked. Immediately upon detecting a captured animal, we recorded its trap location. We combined all trapping data from each month to determine which geographic zones individuals were trapped in most frequently for our analyses.

Upon capture, we first recorded each individual's behavior, first when a human approached the trap (did the individual alarm call, chatter or struggle?) and second, when being handled (willingness to walk into a bag, and defecation when handled). These measures allowed us to obtain a behavioral type of each individual squirrel. Once trapped, the individual was placed into a handling bag where it was weighed in grams, and its sex was determined based on visual inspection of the external genitalia. Two species of fleas (*Oropsylla montana*, *Hoplopsyllus anomalous*) were collected and counted following the protocol from Smith et al. (2021).

The first time that an animal was captured, it was marked with a uniquely numbered metal ear tag (National Band and Tag Co., Newport, Kentucky), and a Passive Integrated Transponder (PIT) tag (Biomark, Inc., Boise, Idaho; for details, see Smith et al., 2018 for details), and a unique mark was painted on its back using Nyanzol cattle dye. All procedures were approved by the IACUC Committee at Mills College, the University of Wisconsin IACUC protocol #333, and the University of California at Davis IACUC protocol #19853 and are consistent with the guidelines of the American Society of Mammologists for the use of wild mammals in research (Sikes 2016).

Statistical Analysis

We conducted robust design capture-mark recapture analysis on 9 years of trapping data to estimate apparent survival (*S*; the product of true survival and permanent emigration) using Huggins full heterogeneity models (Huggins 1989, 1991). Capture-mark recapture analysis uses capture histories for each individual corresponding to whether an individual was captured within a sampling period (constructed with 0s and 1s). The advantage of this type of analysis is that it allows for estimation of other biologically important reasons why an animal might be captured or not, including temporary migration patterns (*Gamma'*; the probability that an individual temporarily left the study period given that it was alive and captured in the previous sampling period) and the probabilities of being captured (*p)* and recaptured (*c*).

The robust design involves sampling during primary and secondary periods. Our primary periods consisted of months and our secondary periods consisted of multiple trapping days within each month (Appendix Table S3.1). Primary periods are often separated by longer intervals and assumed to have no births or deaths within primary periods (‘closed’) and open (i.e., births and deaths occur) between primary periods (Nicholson et al. 2012). These models assume the following null hypotheses: (1) marks are unique, permanent, and identified correctly, (2) all individuals have equal probability of being captured within a sampling period, (3) each individual’s probability of capture is independent of others, (4) the population is closed within primary periods and (5) all individuals have equal probability of survival. The point of our analysis is to identify ‘violations’ of assumption 5; e.g., to quantify how sex, age and various covariates might affect apparent survival. To do so, we ran separate models for each sex (Sprogis et al. 2016) to explore if the covariates that influence our parameters of interest differ for males and females. To account for age differences, we limited our data to only include individuals who were first captured as juveniles (<1 year of age). Thus, upon first capture each individual was assigned an age, in months, of zero. This allowed us to assign an exact age to each individual in our study.

To minimize violations of assumptions 1-4, we took the following steps. First, we used three distinct ways (see methods above) to identify squirrels accurately at trapping events. Second, we placed traps evenly across the study population to increase trapping success across our study population and trapped regularly within each sampling period to ensure all squirrels were detected (Appendix Table S3.1). Third, within any given primary period (one month), it is unlikely an individual will permanently leave the study area and most births occur prior to our trapping periods. Lastly, we recognized certain life-history traits are likely to violate the assumption of equal probability of survival such as sex and age. Thus, we took a sex-specific modelling approach and ran separate models for each sex (Sprogis et al. 2016) to explore if the covariates that influence our parameters of interest differ for males and females. To account for age differences, we limited our data to only include individuals who were first captured as juveniles (<1 year of age). Thus, upon first capture each individual was assigned an age, in months, of zero. This allowed us to assign an exact age to each individual in our study.

For our analysis we included the following covariates in our models for each individual: human disturbance, age, body condition, flea load, behavioral type measures (see the next paragraph), and time. For human disturbance, we determined the location that the individual was trapped most within the primary period and associated that with a high or low human disturbance value depending on whether it fell above or below the disturbance mean for that period. Except for behavioral scores which were calculated once for each individual in a given year (see below), we calculated separate measures for each individual-level covariate for each primary period (i.e., human disturbance, body condition, and flea load) using an average from all secondary period events (e.g., mean body condition within one month). Our 'time' covariate was allowed to vary with each primary period and encompasses the environmental variables we were unable to measure across the years.

For our behavioral scores, we obtained binary measures at each trapping and handling event recorded as 0 (did not perform behavior) or 1 (performed behavior). We then summed scores for each behavior for all trapping events within a season and divided it by the total number of times trapped within a season. Thus, each individual had a proportional score for each trapping and handling behavior for every year they were trapped. To reduce the dimensionality of our correlated behavioral measures, we ran multiple factor analysis (MFA) using package FactoMineR (Lê et al. 2008) to create fewer numbers of uncorrelated variables combining behaviors when in a trap ("trapping behaviors") and when being handled ("handling behaviors").

The first two dimensions explained 58% of the total variation (36.9% and 21.1% respectively; Appendix Table S3.2). The first dimension (hereafter "dim1") correlates with struggling and chattering in the trap and willingness to walk directly into a bag during handling. The second dimension (hereafter "dim2") correlates with an increase in the propensity to alarm call when approached in the trap and a decrease in the tendency to defecate while being handled.

We also ran models that included interactions between human disturbance and body condition, flea load, dim1, and dim2. The combination of all possible covariates of interest is shown in figure 3.2 and resulted in 10,400 models. All statistical analyses were performed in R version 4.2.1 (R Core Team 2021) using package RMark (Laake 2013). Prior to analysis, all numerical variables were standardized around their means and multicollinearity of our covariates was checked using package "usdm" (Naimi et al. 2014). The Akaike information criterion corrected for sample size (AIC_c) was used to estimate relative model support, the model with the lowest AICc was selected as the best fit (Kendall 2011). All models within four units of the best fitted model were averaged to obtain the unbiased apparent survival parameter estimates shown for covariates of interest (White et al. 2001).

Results

We trapped a total of 551 unique individuals (258 male; 293 female) over the course of our 9-year study period. The best fit models for males versus females are presented in Appendix Table S3.3. Table 3.1 displays the AICc weights of each covariate mix derived from all possible parameter and covariate combinations.

For male squirrels, we found that older individuals, and those residing in areas of higher human disturbance had higher apparent survival rates (Figure 3.3a; Table 3.1). In particular, young males in areas of low human disturbance had the lowest apparent survival rates. In contrast, we found an interactive effect between human disturbance and age for females (Table 3.1). Younger females tended to have slightly higher apparent survival rates in areas with high human disturbance, while older females exhibited slightly lower apparent survival in these areas (Figure 3.3b). Predicted real estimates revealed that overall, females had higher apparent survival rates than males (Table 3.2). The lower apparent survival of males may be attributed to their dispersal tendencies rather than true low survival rates. This is further supported by our finding that males after the presumed age of dispersal (i.e., years 2 & 3), had comparable apparent survival estimates to females (Table 3.2).

Apparent survival was also influenced by different aspects of behavioral type in ways that depended on age and sex. Males who alarm called frequently when approached by humans had lower apparent survival rates across all age groups, but particularly for older males (Figure 3.4a). For female squirrels, a different aspect of behavior, the tendency to do more chattering and struggling in the trap, was associated with lower apparent survival rates (Figure 3.4b). Similar to males, this relationship was age-dependent; however, in the opposite way. The tendency for females to have lower apparent survival with higher loadings on dimension 1 was most clear for younger females and not for older ones. Body condition and flea load did not have substantial weight in our top models (Appendix Table S3.4).

Discussion

While studies have suggested that the increase in human presence within natural environments may have detrimental effects on wildlife survival (Geffroy et al. 2015), our findings suggest that human presence within a semi-urban park increased apparent survival in the California ground squirrel, either due to reduced mortality or reduced emigration. Other studies have found that animals living in more human-dominated landscapes tend to have higher survival rates due to decreased predation pressures (Rebolo-Ifran et al. 2015). Our findings further support the theory that humans provide animals a place of safety and refuge from natural predators (Berger 2007, Suraci et al. 2019, Lamichhane et al. 2023). However, it is important to consider that human presence within these natural landscapes may be beneficial for individual survival yet may have broader population-level implications including increased inbreeding and intraspecific competition.

Within our site, male ground squirrels exhibited higher apparent survival rates when residing in areas with higher levels of human disturbance. This suggests humans may be potentially altering true survival for male individuals (i.e., decreasing mortality rates) or reducing their likelihood of dispersing to new habitats, as observed in other species (Doherty et al. 2021). Similarly, we found younger females squirrels displayed slightly higher apparent survival rates when residing in areas of high human disturbance. However, this trend reversed for adult females greater than the age of three years, where older females had lower apparent survival rates in our high human disturbed zone. One possible explanation for this difference could be the reproductive costs associated with older females. Previous studies have found that animals living in urban areas show changes in their reproductive timing, often breeding earlier and/or longer due to increased resources (Lowry et al. 2013). Within the higher human disturbed zone with decreased predation risk (Ortiz-Jimenez et al., in prep), females may be allocating more resources towards reproductive effort, which could influence their survival.

Although overall we found females had higher apparent survival rates than males, we cannot definitively conclude that females are surviving better than males. Instead, male ground squirrels may be dispersing from the site, although less frequently than previously reported (Stroud 1982). Pilot data on California ground squirrels suggests juvenile males only emigrate at distances from 150 m to over 600 m, with most males remaining within 300 m from their natal burrow (Stroud 1982, Dobson 2016). Thus, dispersal distances are short enough to occur within the spatial scale of our study population. That in combination with the fact that our overall apparent survival rates were very high suggests our results are likely capturing rates of true survival for male ground squirrels with minimal dispersal out of the study site. Still, as juveniles, males had much lower apparent survival rates than females. According to our model predictions, it appears males in this population exhibit a decrease in apparent survival rates from 95% in year 1 to 90% in year 2 (Table 3.2). These finding indicate that either males have lower survival compared to females as juveniles, or male ground squirrels from this population have two main times of dispersal which may be dependent on another factor such as body condition (Holekamp 1986, O'Riain et al. 1996).

We found that the behavioral types displayed by male and female ground squirrels when approached or handled by a human were associated with differences in apparent survival rates. Specifically, females displaying behaviors such as struggling and chattering (dim1) tended to have lower apparent survival, but this trend was only significant for females in their first two years of life. On the other hand, males displaying alarm calling behavior (dim2) was associated with lower apparent survival, and this effect was more pronounced in older males above the age of two. Previous studies have also found conflicting findings on the relationship between personality and survival (Turner et al. 2020, Moiron et al. 2020), and our study adds further complexity showing the importance of behavioral type on apparent survival among certain age classes. Overall, however, the reaction of animals to humans while trapped can provide valuable insights into their perception of humans compared to non-human predators. These findings contribute to our understanding of how animals evaluate and respond to potential threats in their environment and how that may be associated with survival in wildlife populations.

Interestingly, among all the factors we examined, human disturbance and age were the highest weighted predictors of apparent survival surpassing body condition and flea load, which carried minimal weight across our models. While body condition intuitively plays an important role in survival and dispersal, the safety humans provide within the environment, potentially by scaring off natural predators, outweighs these individual-level traits.

Our long-term study on the California ground squirrel provides valuable insights into the effects of human disturbance on small mammal mortality and emigration. While human disturbance has historically been assumed to have a detrimental impact on wildlife survival, our study highlights the potential benefits human presence can provide to small mammal species. Further, there has been limited investigation into the combined influence of factors such as sex, age, body condition, personality, and parasite load on the survival of small mammals in human-altered environments. By examining these factors in combination, we were able to reveal the complex interplay between individual-level traits and ecological processes in shaping apparent survival in a small mammal. By studying the effects of human disturbance on small mammals, we gain valuable insights into how human presence can act as a selective pressure and shape the dynamics of animal populations. This knowledge is essential for conservation efforts and informing management strategies to mitigate the negative impacts of human activities on wildlife.

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Table 3.1. Akaike weights of covariates calculated from all possible parameter and covariate combinations resulting in 10,400 models.

Covariate	AICc
Females	
~human disturbance* age	0.2970
~dim1 * age	0.1442
~flea load + age	0.1253
~human disturbance + age	0.1053
~dim2 + age	0.0786
Males	
~human disturbance + age	0.7229
~dim2 * age	0.1128
~body condition + human disturbance	0.0664
~human disturbance * age	0.0355
~body condition * human disturbance	0.0282

A "+" within the model indicates an additive effect, while a "*" indicates an interactive effect

Table 3.2. Real estimates and 95% confidence intervals of apparent survival from the best fitted top models for female and male ground squirrels.

Age	Estimate (95% CI)	
	Female	*Male*
0	0.94 (0.92-0.96)	0.82 (0.77-0.87)
1	0.98 (0.92-0.99)	0.95 (0.90-0.97)
2	0.97 (0.92-0.99)	0.90 (0.82-0.95)
3	0.98 (0.88-0.99)	0.98 (0.81-0.99)

Figure captions

Figure 3.1. a) Landscape view of study site at Briones Regional Park. b) Plot depicting the average number of visits per hour by humans on the south and north ends of the study site. Error bars represent standard error.

Figure 3.2. Set of Huggins full heterogeneity models considered to assess apparent survival rates in the California ground squirrel population, while controlling for temporary emigration and differences in capture and recapture probabilities. The notation (.) indicates that a parameter was kept constant; (time) indicates that the parameter was allowed to vary with the primary period (months); (mixture) allowed for individual heterogeneity in capture and recapture probabilities (when pi was constant).

Figure 3.3. Predicted real estimates from our top models (within 4 AICc units of the lowest model) depicting apparent survival across our human disturbance zones for a) males and b) females. Each plot is grouped by age with 0 being juvenile squirrels recently emerged from their burrows (0-3 months) and the subsequent years following (year 1 = 3-15 months, year 2 = 15-27 months, etc.). Error bars represent 95% confidence intervals.

Figure 3.4. Predicted real estimates from our top models (within 4 AICc units of the lowest model) depicting apparent survival and **a)** dimension 2 in males and **a)** dimension 1 in females. Each linear prediction is grouped by age class with 0 being juvenile squirrels recently emerged from their burrows (0-3 months) and the subsequent years following (year 1 = 3-15 months, year 2 = 15-27 months, etc.).

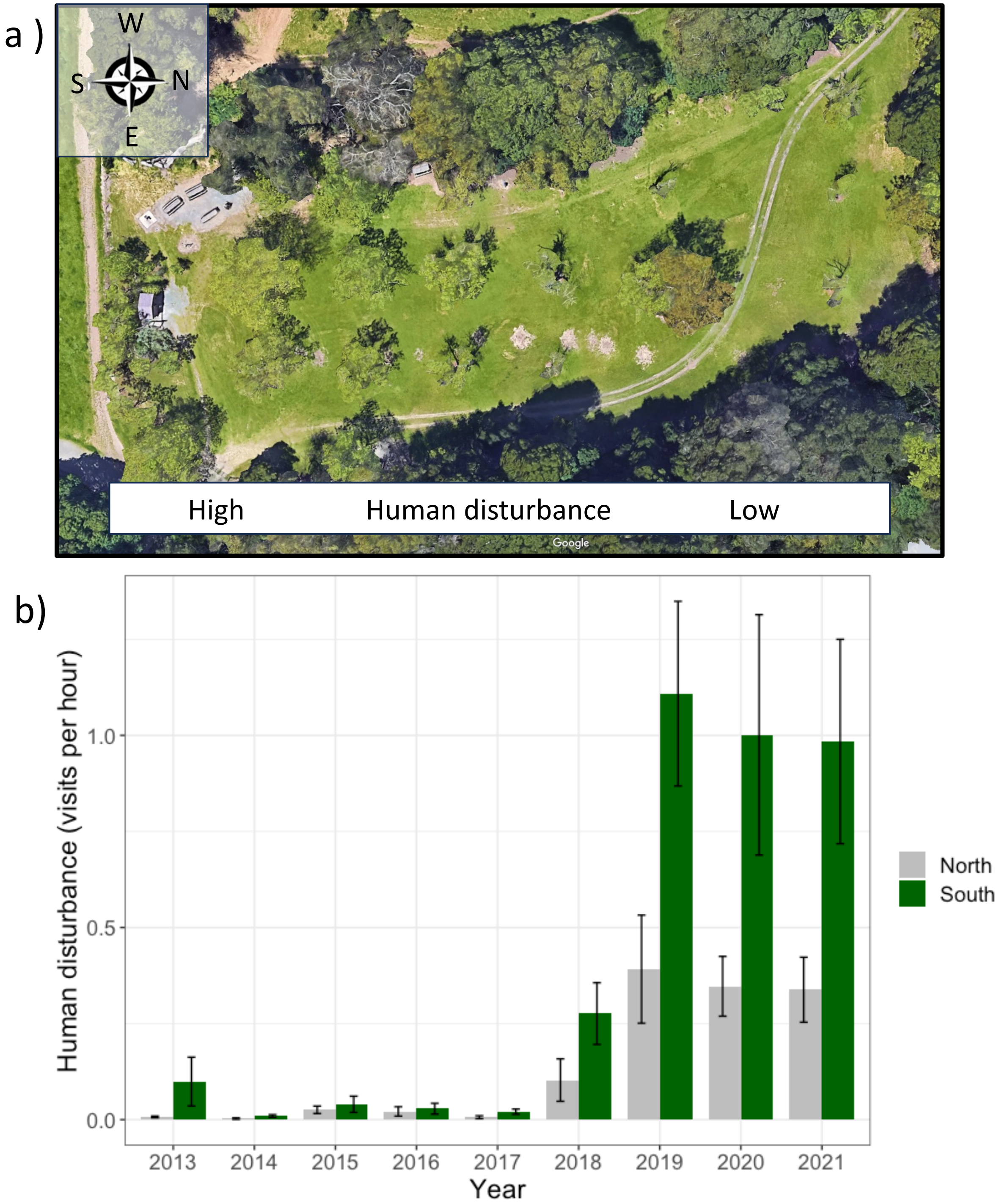

a)
W
S
N
E
High
Human disturbance
Low
Google
b)
Human disturbance (visits per hour)
1.0
0.5
0.0
2013
2014
2015
2016
2017
2018
2019
2020
2021
Year
North
South

Figure 3.1.

$$\left\{\begin{matrix} S(.)\\ S(age)\\ S(body\ condition)\\ S(flea\ load)\\ S(Dim1)\\ S(Dim2)\\ S(time)\\ S(human\ dist)\\ S\left(age * \begin{pmatrix} body\ condition\\ flea\ load\\ Dim1\\ Dim2\\ human \end{pmatrix}\right.\\ S\left(age + \begin{pmatrix} body\ condition\\ flea\ load\\ Dim1\\ Dim2 \end{pmatrix}\right.\\ S\left(human\ dist * \begin{pmatrix} body\ condition\\ flea\ load\\ Dim1\\ Dim2 \end{pmatrix}\right.\\ S\left(human\ dist + \begin{pmatrix} body\ condition\\ flea\ load\\ Dim1\\ Dim2 \end{pmatrix}\right. \end{matrix}\right\} * \left\{\begin{matrix} Gamma'(.) = Gamma''(.)^{*}\\ Gamma'(age) = Gamma''(age)^{*}\\ Gamma'(body\ condition) = Gamma''(body\ condition)^{*}\\ Gamma'(flea\ load) = Gamma''(flea\ load)^{*}\\ Gamma'(Dim1) = Gamma''(Dim1)^{*}\\ Gamma'(Dim2) = Gamma''(Dim2)^{*}\\ Gamma'(time) = Gamma''(time)^{*}\\ Gamma'(human\ dist) = Gamma''(human\ dist)^{*}\\ \begin{pmatrix} Gamma'(.)\\ Gamma'(age)\\ Gamma'(body\ condition)\\ Gamma'(flea\ load)\\ Gamma'(Dim1)\\ Gamma'(Dim2)\\ Gamma'(time)\\ Gamma'(human\ dist) \end{pmatrix} * \begin{pmatrix} Gamma''(.)\\ Gamma''(age)\\ Gamma''(body\ condition)\\ Gamma''(flea\ load)\\ Gamma''(Dim1)\\ Gamma''(Dim2)\\ Gamma''(time)\\ Gamma''(human\ dist) \end{pmatrix}^{**}\\ Gamma' = Gamma'' = 0^{***} \end{matrix}\right\} * \left\{\begin{matrix} p(.) * c(.) * (pi = 1)\\ p(mixture) * c(mixture) * pi(.)\\ p(age) * c(age) * pi(.)\\ p(body\ condition) * c(body\ condition) * pi(.)\\ p(flea\ load) * c(flea\ load) * pi(.)\\ p(Dim1) * c(Dim1) * pi(.)\\ p(Dim2) * cDim2 * pi(.)\\ p(time) * c(time) * pi(.)\\ p(human) * c(human\ dist) * pi(.) \end{matrix}\right\}$$

S	apparent survival between primary periods
Gamma’’	probability of leaving the study area between primary periods
Gamma’	probability of staying outside the study area
p	capture probability
c	recapture probability
pi	mixture parameter, allowing for heterogeneity in *p* and *c*; *pi* = 1 enforces no heterogeneity

* Random temporary emigration (*Gamma’’* = *Gamma’*)

** Markovian temporary emigration (*Gamma’’*≠*Gamma’*)

*** No temporary emigration (*Gamma’’* = *Gamma’* = 0)

Figure 3.2

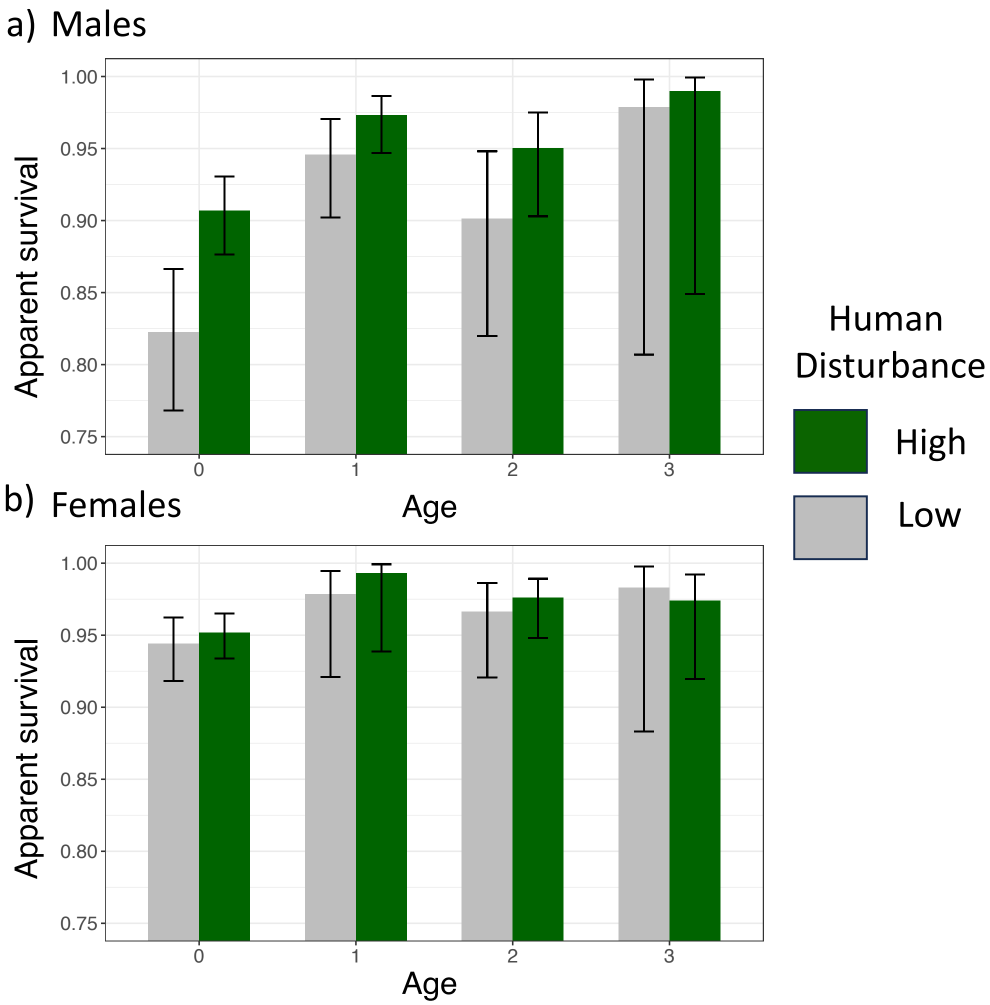
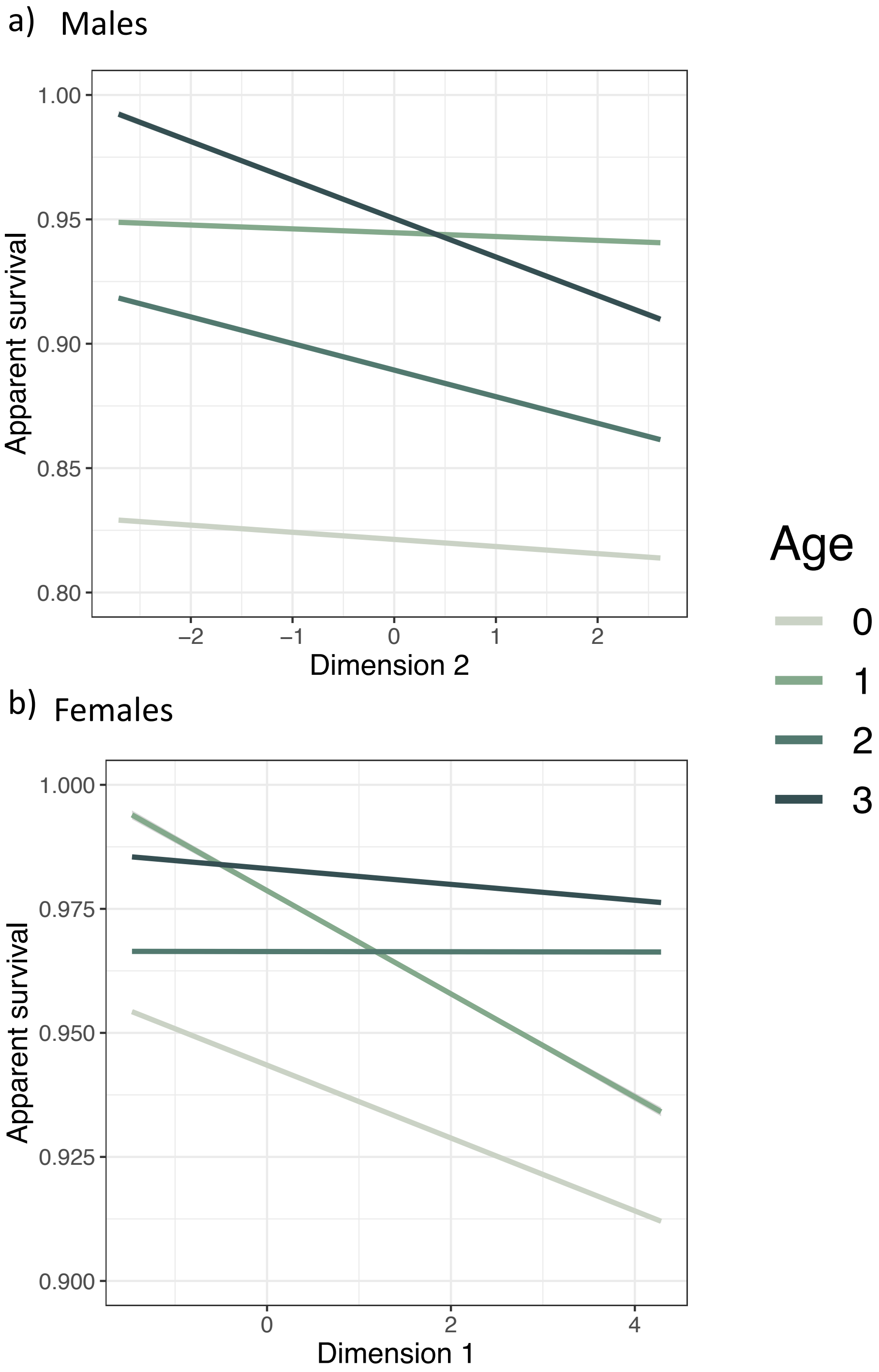

a) Males
Apparent survival
1.00
0.95
0.90
0.85
0.80
0.75
0
1
2
3
Age
b) Females
Apparent survival
1.00
0.95
0.90
0.85
0.80
0.75
0
1
2
3
Age
Human Disturbance
High
Low

Figure 3.3.


a) Males

b) Females

Figure 3.4

Appendix

Table S3.1. Trapping effort across 9 years of this study.

Year	Months	Trapping Effort (total days)
2013	June - July	11
2014	May - July	15
2015	May - July	26
2016	May - July	20
2017	May - July	28
2018	May - July	22
2019	May - July	26
2020	June - July	26
2021	May - July	23
2022	May - July	15

Table S3.2. Multiple factor analysis (MFA) results for behaviors displayed by ground squirrels in the trap and while handling. Bolded values aligned most strong with dimension 1 or dimension 2, respectively.

Behavior	**Dim.1 (36.9%)**	**Dim.2 (21.1%)**
Behavioral defecation	0.5333165	**-0.568837**
Walked into bag	**0.7541134**	-0.2030635
Chattered	**0.6522313**	0.1961276
Struggled	**0.6675184**	0.3246811
Alarm called	0.2019846	**0.7589519**

Table S3.3. Top capture-recapture models fitted to the capture histories of ground squirrels to estimate parameters for apparent survival (*S*), temporary migration (*Gamma''*), permanent migration (*Gamma'*) and capture (*p*) recapture (*c*) probabilities. All top models fall within 4 units of the model with the lowest Akaike weight (AICc).

Model	AICc	ΔAICc	AICc weight
Female			
S(~hd * age)Gamma"(~time)Gamma'(~1)pi(~1)p(~mixture)c(~mixture)	12926.752	0.000	0.106
S(~td1 * age)Gamma"(~time)Gamma'(~1)pi(~1)p(~mixture)c(~mixture)	12928.195	1.443	0.052
S(~fl + age)Gamma"(~time)Gamma'(~1)pi(~1)p(~mixture)c(~mixture)	12928.479	1.727	0.045
S(~hd * age)Gamma"(~time)Gamma'(~bd)pi(~1)p(~mixture)c(~mixture)	12928.806	2.054	0.038
S(~hd * age)Gamma"(~time)Gamma'(~fl)pi(~1)p(~mixture)c(~mixture)	12928.806	2.054	0.038
S(~hd * age)Gamma"(~time)Gamma'(~hd)pi(~1)p(~mixture)c(~mixture)	12928.806	2.054	0.038
S(~hd * age)Gamma"(~time)Gamma'(~td1)pi(~1)p(~mixture)c(~mixture)	12928.806	2.054	0.038
S(~hd * age)Gamma"(~time)Gamma'(~td2)pi(~1)p(~mixture)c(~mixture)	12928.806	2.054	0.038
S(~hd + age)Gamma"(~time)Gamma'(~1)pi(~1)p(~mixture)c(~mixture)	12928.828	2.076	0.038
S(~td2 + age)Gamma"(~time)Gamma'(~1)pi(~1)p(~mixture)c(~mixture)	12929.430	2.678	0.028
S(~td1 + age)Gamma"(~time)Gamma'(~1)pi(~1)p(~mixture)c(~mixture)	12929.462	2.710	0.027
S(~age)Gamma"(~time)Gamma'(~1)pi(~1)p(~mixture)c(~mixture)	12929.973	3.221	0.021
S(~td1 * age)Gamma"(~time)Gamma'(~bd)pi(~1)p(~mixture)c(~mixture)	12930.251	3.499	0.018
S(~td1 * age)Gamma"(~time)Gamma'(~fl)pi(~1)p(~mixture)c(~mixture)	12930.251	3.499	0.018
S(~td1 * age)Gamma"(~time)Gamma'(~hd)pi(~1)p(~mixture)c(~mixture)	12930.251	3.499	0.018
S(~td1 * age)Gamma"(~time)Gamma'(~td1)pi(~1)p(~mixture)c(~mixture)	12930.251	3.499	0.018
S(~td1 * age)Gamma"(~time)Gamma'(~td2)pi(~1)p(~mixture)c(~mixture)	12930.251	3.499	0.018
S(~fl + age)Gamma"(~time)Gamma'(~bd)pi(~1)p(~mixture)c(~mixture)	12930.530	3.778	0.016
S(~fl + age)Gamma"(~time)Gamma'(~fl)pi(~1)p(~mixture)c(~mixture)	12930.530	3.778	0.016
S(~fl + age)Gamma"(~time)Gamma'(~hd)pi(~1)p(~mixture)c(~mixture)	12930.530	3.778	0.016
S(~fl + age)Gamma"(~time)Gamma'(~td1)pi(~1)p(~mixture)c(~mixture)	12930.530	3.778	0.016
S(~fl + age)Gamma"(~time)Gamma'(~td2)pi(~1)p(~mixture)c(~mixture)	12930.530	3.778	0.016
Male			
S(~hd + age)Gamma"(~bd)Gamma'(~1)pi(~1)p(~mixture)c(~mixture)	7173.209	0.000	0.169
S(~hd + age)Gamma"(~td2)Gamma'(~1)pi(~1)p(~mixture)c(~mixture)	7174.562	1.353	0.086
S(~hd + age)Gamma"(~bd)Gamma'(~bd)pi(~1)p(~mixture)c(~mixture)	7175.244	2.035	0.061
S(~hd + age)Gamma"(~bd)Gamma'(~fl)pi(~1)p(~mixture)c(~mixture)	7175.244	2.035	0.061
S(~hd + age)Gamma"(~bd)Gamma'(~hd)pi(~1)p(~mixture)c(~mixture)	7175.244	2.035	0.061
S(~hd + age)Gamma"(~bd)Gamma'(~td1)pi(~1)p(~mixture)c(~mixture)	7175.244	2.035	0.061
S(~hd + age)Gamma"(~bd)Gamma'(~td2)pi(~1)p(~mixture)c(~mixture)	7175.244	2.035	0.061
S(~td2 * age)Gamma"(~bd)Gamma'(~1)pi(~1)p(~mixture)c(~mixture)	7176.109	2.900	0.040
S(~hd + age)Gamma"(~td2)Gamma'(~bd)pi(~1)p(~mixture)c(~mixture)	7176.597	3.388	0.031

S(~hd + age)Gamma"(~td2)Gamma'(~fl)pi(~1)p(~mixture)c(~mixture)	7176.597	3.388	0.031
S(~hd + age)Gamma"(~td2)Gamma'(~hd)pi(~1)p(~mixture)c(~mixture)	7176.597	3.388	0.031
S(~hd + age)Gamma"(~td2)Gamma'(~td1)pi(~1)p(~mixture)c(~mixture)	7176.597	3.388	0.031
S(~hd + age)Gamma"(~td2)Gamma'(~td2)pi(~1)p(~mixture)c(~mixture)	7176.597	3.388	0.031

td1 = dim1; *td2* = dim2; *hd* = human disturbance; *mixture* = heterogeneity in capture and recapture probabilities

A "+" within the model indicates an additive effect, while a "*" indicates an interactive effect

Table S3.4. Akaike weights of survival covariates calculated from all possible parameter and covariate combinations resulting in 10,400 models. Bolded values are the highest weighted covariates from all models.

Covariate for survival parameter	**Female**	**Male**
~1	7.753E-06	2.821E-08
~age	5.941E-02	6.812E-04
~body condition	2.217E-03	6.012E-04
~body condition * age	9.934E-03	1.301E-03
~body condition * human disturbance	1.645E-03	2.820E-02
~body condition + age	3.720E-02	6.936E-04
~body condition + human disturbance	3.551E-03	6.636E-02
~flea load	2.827E-06	2.988E-07
~flea load * age	3.835E-02	3.211E-03
~flea load * human disturbance	4.473E-05	4.333E-06
~flea load + age	1.253E-01	1.652E-03
~flea load + human disturbance	7.440E-06	7.952E-06
~human disturbance	1.945E-05	1.122E-06
~human disturbance * age	**2.970E-01**	3.555E-02
~human disturbance + age	1.053E-01	**7.229E-01**
~dim1	6.171E-06	1.800E-07
~dim1 * age	**1.442E-01**	5.478E-05
~dim1 * human disturbance	4.954E-06	3.968E-06
~dim1 + age	7.666E-02	3.650E-04
~dim1 + human disturbance	1.295E-05	4.515E-06
~dim2	9.541E-06	1.210E-07
~dim2 * age	2.041E-02	1.128E-01
~dim2 * human disturbance	1.323E-05	1.997E-06
~dim2 + age	7.862E-02	2.556E-02
~dim2 + human disturbance	1.977E-05	4.304E-06
~time	2.608E-09	3.103E-09